Applying a Novel State-Space Stock Assessment Framework Using a Fisheries-Dependent Index of Fishing Mortality

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Abstract

State-space models have a hierarchical framework that assumes the observed data are derived from a time series of unobserved latent states. State-space stock assessment models have emerged as an alternative framework to conduct stock assessment in Canada, the east coast of the United States of America, and in Europe though little research has investigated where and how they are optimally used and if they would be appropriate in other geographical contexts. We built a novel state-space stock assessment model with process variation in recruitment and time- and age- specific catchability. We fit the model to commercial trap net and gill net catch and effort data of Lake Michigan lake whitefish using a marginal likelihood that integrated over latent states. Compared to the previously employed statistical catch at age model, the state-space model estimated dome-shaped, rather than asymptotic selectivity for both fisheries, 15% lower average total instantaneous mortality, and 20% higher average recruitment. To our knowledge this is the first application of a state-space stock assessment model fit by maximum likelihood in the Laurentian Great Lakes and the first such model to not include a fisheries-independent survey. These results demonstrate the feasibility of employing a maximum likelihood state-space framework in fisheries that lack such fishery independent indices of abundance and instead use catch per unit effort as an index of abundance. This work presents a novel approach to applying state-space stock assessment modeling and offers insights and suggestions for future in the Great Lakes and in similar circumstances of data availability.

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State-space stock assessment model,
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36 None

1. Introduction

Fisheries stock assessment must contend with multiple sources of model variability, both from the process sub-model (i.e., process variation) and from the observation sub-model (i.e., observation error) which introduce uncertainty and obscure the relationship between underlying model dynamics and the observed data (Fournier and Archibald, 1982). Until recently, age-structured fisheries stock assessment models have generally assumed the degree of process variation and/or observation error was known. Deriso *et al.* (2007) emphasized that it is possible to estimate the variances, even from multiple sources, when all variation is due to observation error. If process variation is present and deviations from the mean are treated like another source of data, the variance of those deviations cannot be independently estimated by maximizing the joint likelihood of the deviations and data, a procedure sometimes called penalized likelihood (see Schnute 1994). The penalized likelihood, also called "errors-in-variables" (EV) method, is still used in many stock assessment packages such as ASAP, MULTIFAN-CL, and stock synthesis (SS) (Fournier et al., 1998; Legault and Restrepo, 1998; Methot and Wetzel, 2013). However, because the estimates can be asymptotically biased, alternative approaches have been adopted in newer assessment platforms (de Valpine and Hilborn, 2005; Stock and Miller, 2021). State-space models (SSM) have been able to partition process variation and observation error and estimate both with high precision (Aeberhard et al., 2018). SSM accomplish this by assuming the data are observations (with error) derived from unobserved states like population abundance and mortality, that are progressing through time following a stepwise Markovian process. The states, or their deviations from a shared mean, are specified as random effects and in a maximum likelihood framework are integrated over to obtain the marginal likelihood, which is maximized.

The theorized advantages of state-space stock assessment models have been realized, with models applied in several different geographical regions, using different model configurations, able to simultaneously estimate the magnitude of several different sources of process variation, including recruitment, survival, fishing mortality, selectivity, and natural mortality (Aeberhard et al., 2018; Cadigan, 2015; Stock et al., 2021; Stock and Miller, 2021; Yin et al., 2019). State-space stock assessment models (herein defined as those that use a marginal likelihood) have estimated mortality and abundance with less bias and higher precision than in non-state-space models (herein defined as those that use a penalized likelihood), and exhibit less retrospective bias (Gunnlaugsson, 2012; Perreault et al., 2020; Stock et al., 2021). A state-space modeling research track is currently exploring the feasibility of applying such models to NOAA-managed stocks in New England and the Mid-Atlantic and state-space stock assessment models are used for a large portion of stocks managed by the International Council for the Exploration of the Sea (ICES) (Aanes et al., 2020). Nevertheless, there remains considerable interest and uncertainty in what kinds of process variation can be considered, and under what circumstances and with what data the SSM approach can be practically implemented (Aanes et al., 2020).

This work contributes to the ongoing inquiry by using a state-space modeling framework to fit total catch and age composition data for a multi-gear fishery without a fisheries-independent index of abundance. Indices quantify trends in stock abundance over time and are often assumed to be proportional to abundance therefore allowing an estimation of stock size. In the absence of a fisheries independent survey, an index can be calculated from data collected during the fishing process, such as catch per unit effort (CPUE). However, CPUE is only a reliable index of abundance if the proportionality constant, catchability, is correctly specified (Wilberg et al., 2009). Catchability is often assumed constant or varying around a constant mean, though can vary systematically due to density-dependent effects, gear changes, preferential sampling, or angler behavior (Ducharme-Barth et al., 2022; Hilborn and Walters, 1992; Quirijns et al., 2008). In such cases, potential causes of changes in catchability might be unknown, but can still be partially accounted for by allowing catchability to vary through a stochastic process, an approach we adopt herein (Wilberg et al., 2009).

This novel state-space model was applied to lake whitefish (*Coregonus clupeaformis*) in the northmost region of Lake Michigan. This stock experiences no recreational fishing and two commercial fisheries, a trap net fishery and a gill net fishery, have yielded on average 222 and 159 thousand kilograms per year, respectively, since 1986, the first year included in the assessment. Fishing effort is reported in numbers of lifts of the trap nets and feet of gill net deployed. These effort data were used to inform fishing mortality within the model and catchability was a state variable estimated for each age and year that scaled effort to fishing mortality. This parameterization distinguishes this state-space model from previous applications and existing state-space platforms like SAM or WHAM where instantaneous fishing mortality is a state variable (Nielsen and Berg, 2014; Perreault et al., 2020).

To our knowledge, this is the first state-space stock assessment model application in the Laurentian Great Lakes (fit by marginal maximum likelihood) and this work confirms the applicability of SSM without a fisheries independent survey, which is customary in previous applications (Cadigan, 2015; Nielsen et al., 2021; Perreault et al., 2020; Stock and Miller, 2021). Our objective was to apply a novel state-space stock assessment model, provide time- and age-varying estimates of recruitment and catchability and their associated variances. Ultimately, we developed an assessment tool applicable in situations without fisheries independent surveys and make general recommendations about the use of SSM models in such situations.

2. Methods

2.1 Data and Model Inputs

The assessment model was fit using annual fishery-specific values of fishing effort ($E_{y,G}$), observed fishery harvest ($\tilde{C}_{y,G}$), and observed age compositions in units of proportions at age ($\tilde{P}_{a,y,G}$) (variables are described in Table 1). Annual reported yield in weight from the catch reporting system was converted into estimates of annual catch in numbers using the annual average weight of fish harvested by each fishery and estimates of underreporting (Appendix A). In addition, the model used input values of average weight at age, average length at age, and maturity schedules in each year, which were collected from harvest subsampling, to calculate selectivity and spawning stock biomass.

State-space Assessment Model

A state-space stock assessment model (SSM) was developed in Template Model Builder (TMB) that assumed two state variables, recruitment and catchability at age, varied across years (Kristensen et al., 2016). The SSM was structurally similar to the existing statistical catch at age (SCA) models used to assess lake whitefish and lake trout in the Laurentian Great Lakes which fit data using a penalized likelihood (described in Appendix B). The SSM had structural elements that mimicked the state-space modeling software "SAM" including the state variables, process variance structure, and a marginal likelihood (Berg and Nielsen, 2016; Nielsen and Berg, 2014). The SSM had two sub-models: a process or "population" model, and an observation or "fishery" model. The process model described how the underlying states, recruitment and catchability, progressed over time as a function of the state in the previous year and process variability. The observation model described how the predicted total catch and catch compositions derived from those true unobserved states owing to observation error.

Recruitment was modeled as a random walk which effectively penalizes recruitment estimates that change greatly from year to year with the extent of the penalty depending on the random walk variance. Though recruitment can differ greatly between adjacent years due to several abiotic and biotic processes, treating these changes as arising from random walk is a recommended approach in a state-space framework especially when estimating the variance of the process variability (Maunder and Thorson, 2018). Recruitment, $N_{4,y}$, was calculated on the log-scale by adding normally distributed error to the log-scale recruitment in the previous year, starting 5 years prior to the first year being modeled (Table 2, Eq. 1.1). Abundances of individuals ages 5 to 9 in the initial year, 1986, were calculated using the recruitment from years preceding the time series, 1981-1985, which were estimated by extending the random walk process backwards in time (Eq. 1.2). This method assumed that recruitment prior to 1986 came from the same stochastic process as recruitment throughout the time series and the initial abundances are a function of prior recruitment, adjusted downward using average total mortality. Given that there is no information on mortality rates prior to 1986, the average estimated age-specific instantaneous mortality rates for 1986-1988, $\bar{Z}_a$, were used as reasonable substitutes. The abundance of older ages in the initial year were set to 0, consistent with the very low or zero harvest for cohorts that were age-9 or older in 1986 (Eq. 1.3).

Abundances in subsequent years and ages were a function of an exponential mortality model (Eqs. 1.4-1.5). Instantaneous fishing mortality was the product of age-, year-, and fishery-specific catchability, $q_{a,y,G}$ and year- and fishery- specific effort, $E_{y,G}$ (Eq. 1.6a), a common approach in stock assessment models (Fournier and Archibald, 1982). Effectively, $q_{a,y,G}$ combines what is conventionally modeled as two separate processes, year-specific catchability, and age-specific selectivity, into a single age- and year- specific value. Time varying selectivity is commonly used in stock assessment to account for changes in size at age or changes in gear technology that may preferentially target certain ages, among other reasons (Martell and Stewart, 2014). The vector of log-scale catchability at age in a given year, for a given fishery, i.e. $\boldsymbol{q}_{y,G} = (q_{4,y,G}, q_{5,y,G}, \ldots, q_{A,y,G})$, varied over time according to a random walk with multivariate normal error, analogous to how SAM models age specific instantaneous fishing mortality (Eq. 1.7bi) (Nielsen and Berg, 2014). The covariance matrix, $\boldsymbol{\Sigma}$, is a flexible matrix that quantifies the variability and correlation among ages of the year- and fishery- specific process variability vectors, $\boldsymbol{\varepsilon}_y^{(G)}$ (Eq. 1.7bii). Though the covariance matrix can be parameterized in many ways depending on assumed similarity of age-specific process variability, in this model the correlation structure was a first order autoregressive process (AR(1)), where the degree of correlation was a function of the absolute difference in ages. This correlation structure, when applied to fishing mortality or selectivity, has a demonstrably better fit to data in other stocks and is now the default structure in SAM models and a popular option in WHAM models (Berg and Nielsen, 2016; Nielsen et al., 2021; Nielsen and Berg, 2014; Stock and Miller, 2021). The assumption of stronger correlation in catchability variations between adjacent ages, implicit in the AR(1) structure, is sensible given that many factors (such as size or depth distributions of fish) will tend to be more similar for fish closer in age (Nielsen and Berg, 2014). Catchability in this case is expressed as a proportionality between fishing effort and fishing mortality. This is also the proportionality between annual catch and average annual abundance (Ricker, 1975). Thus our assumption that fishing mortality is proportional to fishing effort is equivalent to treating annual catch divided by annual effort as an abundance index.

Fishery-specific correlation coefficients ρ_G and standard deviation, σ_G, parameters were estimated for each fishery and were invariant among ages. The correlation coefficients were estimated on the logit scale, and thus constrained between 0 and 1. These determined how the random walk errors of age-specific catchabilities were related among ages. We did not allow for negative correlations as we could not envision a mechanism that would cause age-specific catchability to differ most for adjacent ages. At one extreme of the allowed range, log-scale catchabilities would change by the same amount for every age from year to year, and their trajectories over time would be parallel ($\rho = 1$). At the other extreme age-specific catchabilities would develop over time completely independently ($\rho = 0$). The estimated value determined the model dynamics between these extremes.

In the observation sub-model, the predicted age-, year-, and fishery- specific catch was calculated using the Baranov catch equation (Eq. 2.1). The predicted proportions at age were derived from those values (Eq. 2.2).

The SSM assessment model was fit by maximizing a marginal (integrated) likelihood. The random effects, ψ, were integrated out of the likelihood, so the objective function was conditional only on the fixed effect parameters, λ. The marginal likelihood contained two components, the likelihood of the data given the random effects and the parameters, $L(\lambda|X,\psi)$, and the probability density function of the random effects, $f(\psi)$,

$$L(\lambda|X) = \int_{-\infty}^{\infty} L(\lambda|X,\psi) f(\psi) d\psi.$$

The likelihood of observing the total catch and catch composition were modeled as a log normal distribution and a multinomial distribution, respectively (Eqs. 3.6-3.7). Estimated age- and year- invariant M was estimated using a normally distributed likelihood with mean $\widetilde{M} = 0.2$ and fixed standard deviation σ_M^2 (Eq. 3.5b). Because of this distribution's inclusion in the likelihood portion of the marginal likelihood, $\widetilde{M}$ is effectively a single observed data point which the model fits by predicting M. Error from the random walk of log-scale recruitment, $\log N_{4,y}$, was assumed to come from a 0-mean normal distribution (Eq. 3.2b). Error in the age- and fishery- specific random walk of catchability was assumed to arise from a 0-mean multivariate normal distribution (Eq. 3.3b). The standard deviations for the observed log-scale total catch by fishery, σ_{CG}, were fixed at 0.067, the values used in the SCA model. These was found in the SCA model by following an iterative procedure during fitting that adjusted the ratios between process and observation error variance, until the target value of σ_{CG} was achieved, as described by (Richards et al., 1997). This effectively means variance was set based on expert judgment at a level that assumes that two-thirds of observed catches would be within about 6.7% of the true values. We fixed σ_{CG} at the same value in the SSM model because the model did not converge when we attempted to estimate it along with the other parameters. We conducted a sensitivity analysis that set σ_{CG} at values 50% above or below 0.067.

The point estimates of fixed effect parameters (including the standard deviation parameters for the random effects) were estimated by maximum likelihood. The predicted random effects and derived quantities (i.e., abundance, spawning stock biomass, mortality) were calculated using the "epsilon" method bias correction algorithm which is now standard in TMB (Thorson and Kristensen, 2016).

2.2 Case Study- Lake Michigan Lake Whitefish

The lake whitefish stock used as a case study for the application of the novel state-space stock assessment is the northmost management region of Lake Michigan, from the Straits of Mackinac to Seul Choix Point, WFM-03 (Fig. 1). Lake whitefish in the Laurentian Great Lakes have experienced a declining recruitment since the 1990s owing to changes in ice cover and food web dynamics (Ebener et al., 2021). Estimated recruitment in WFM-03 has ranged from 1.5 million individuals during peaks in the 90s and early 00s, to less than half a million in the past five years (Caroffino and Seider, 2020). Individuals are recruited to the fishery at age 4, and on average adults are equally susceptible to environmental and biological drivers of natural mortality over time. Changes in environmental conditions that are not fully understood, notably declines in an important food source, *Diporeia*, have driven declines in lake whitefish growth and condition which are reflected in the age, length, and weight data (Fera et al., 2015).

No emigration or immigration was included in the model, because sub-populations in each management unit tend to reproduce in the same region in which they were born, which has been observed from tagging and genetic studies (Ebener et al., 2010; VanDeHey et al., 2009). Two commercial fisheries occur on lake whitefish in WFM-03, a trap net and gill net fishery, both of which are exclusively fished by members of tribes represented by the Chippewa Ottawa Resource Authority (CORA) (Caroffino and Lenart, 2012). Licensed fishers are obligated to report daily weight of landed fish and the amount of gear used (length of gill net or number of trap net lifts), which are aggregated to a single yearly value for the management region (Ebener et al., 2005). The harvest and effort data are not aggregated across both fisheries because several features make the two fisheries unique. The gears tend to exhibit different age-specific selectivity curves; gill nets are dome shaped whereas the trap nets are believed to be asymptotic- catching more older and larger fish than the gill nets (Zhao and Morbey, 2017). Additionally, the temporal patterns of relative effort of the two fisheries differed considerably over time, often due to changes in the market and management actions, including a gill net conversion program, wherein Michigan exchanged fishers' gill nets for trap nets, which was implemented with the 2000 consent decree (*United States vs. Michigan Consent Decree*, 2000). Lastly, an adjustment was necessary to define effective gill net effort because of changes to the average height of gill net gear over time (Ebener et al., 2005).

For Lake Michigan lake whitefish, fisheries management is conducted through regulations intended to limit harvest so as to not exceed a constant annual mortality rate of 65% for any age, and to sustain a spawning potential ratio (SPR) of at least 20% (Ebener et al., 2005). SPR is the ratio between the spawning stock biomass per recruit (SSBR) obtained with the current age-specific fishing mortality schedule held constant over the life of a cohort and the spawning stock biomass per recruit given no fishing mortality ($SSBR_{F=0}$). This equates, conditioned on life-history, to a constant fishing mortality rule because in Lake Michigan for lake whitefish natural mortality is assumed constant. The recommended harvest level is calculated by scaling age-specific fishing mortality rates (averaged over the last three years of the assessment) up or down to meet mortality and SPR conditions in projections.

We compared the estimated abundance, recruitment, spawning stock biomass, and instantaneous mortality, between the SCA and SSM, and determined if differences in output would change management metrics. Spawning stock biomass was the product of proportion mature, average weight at spawning, and abundance at age (Eq. 1.8). The trends of abundance, recruitment, biomass, and mortality were visually compared, and the percent difference of each year-specific value, and the minimum, the maximum, and average over the whole time series were calculated. The ranges (differences between maximum and minimum values) were compared between the SCA and SSM. The patterns of age- and year- specific catchability of the SSM was compared to the catchability and selectivity in the SCA. Because the SCA model estimates annual catchability and age- and year- specific selectivity, the product of these values was compared to the age- and year- specific catchabilities from the SSM. The annual total mortality in the final three years and the SPR based on those mortality rates were compared against the established limits. Other diagnostic values, like normalized one step ahead (OSA) residuals for the age composition data in both the SCA and SSM models, ordinary least squared (OLS) or "Pearson residuals" for the total catch in the SCA model, OSA residuals for the total catch in the SSM model, and retrospective patterns were examined to compare relative model fits (Appendix B and C) (Hurtado-ferro et al., 2015; Trijoulet et al., 2023). OSA residuals account for random effects and the correlation between observations in the multinomial distribution and were calculated either externally (for SCA) or internally (for SSM) as described in Trijoulet et al., (2023). OLS residuals were used to evaluate the SCA model's fit to total catch because these observations are continuous and normally distributed and this model does not have random effects. Mohn's rho statistic was used to quantify the degree of retrospective bias in recruitment and spawning stock biomass and compared against the standard acceptable range for short-lived species, -0.22 to 0.3 (Hurtado-ferro et al., 2015; Mohn, 1999).

3. Results

The SSM converged on a global minimum of the objective function (Eq. 3.1) and estimated the mean and standard error for the fixed effects: instantaneous natural mortality, M, the standard deviations of the process variability, σ_R and σ_G, and the degree of correlation in the process variability of the age-specific catchability for each fishery, ρ_G (Table 3). A visual assessment revealed that the output of the SSM exhibited similar trends as that of the SCA model despite the considerable differences in model configuration (Figs. 3-5). A quantitative comparison between the average, minimum, maximum, and range of derived quantities revealed a -62 to +53% difference in some output values (Table 4).

Abundance and recruitment (abundance at age 4) followed similar trends across time in the two models (Fig. 3). The average abundance in the SSM model was 3 million and in the SCA model it was 2.6 million. Estimates of abundance for both models peaked in 2007 and were lowest in 1989 (Fig. 3A). The range in abundance was smaller in the SSM model. In the SSM the maximum total abundance was 4.3 times larger than the minimum abundance, and in the SCA, the maximum was 4.6 times the minimum. Neither model estimated abundance consistently higher or lower across the entire time series, though the SSM estimates ranged from 11% lower to 64% higher than of those of the SCA model and was larger for most years.

Estimates of recruitment differed more substantially than abundance between the models, though both the SSM and SCA models estimated similar trends (Fig. 3B). Estimated recruitment for both models were greatest in 1995 and lowest in 1988. The range in recruitment was smaller in the SSM. In the SSM the maximum estimated recruitment was 3.8 times larger than the minimum estimate and in the SCA model, the maximum was 6.1 times larger than the minimum. Neither model consistently estimated higher recruitment than the other. Recruitment estimates in the SSM were 14% lower to 103% higher than those of the SCA model (at the very beginning and penultimate point of the time series, respectively). Mean recruitment was 13% larger in the SSM (807,000 versus 889,000, for SCA and SSM respectively) and 32% larger in just the final 10 years (492,000 versus 633,000, for SCA and SSM respectively). In the final 5 years, the SSM estimated a positive trend and the SCA model a negative trend.

Both models estimated similar trends in spawning stock biomass (SSB), except for near the end of the time series, when the SSM estimates rose and the SCA estimates fell (Fig. 4). In both models, the maximum SSB occurred in 1998 and the minimum in 1989, and in both the maximum value was approximately 2.7 times larger than the minimum. SSM estimates of SSB ranged from 10% lower to 59% higher than those of the SCA model, and the average difference was 15%. The mean SSB was 3.9 million lbs. for the SSM and 4.5 million lbs. for the SCA. For both models the trends in SSB were different from trends in abundance and recruitment due to temporal patterns in mortality and weight at age.

In both models, the total instantaneous mortality rate initially increased in the first third of the time series, then a gradually declined (Fig. 5). The SCA model estimated higher mortality than the SSM for most of the time series, reaching a maximum in 1993 at an instantaneous total mortality rate of 1.288 yr^{-1} (averaged across ages 4-15+) (Fig. 5A). The SSM reached a maximum total mortality in the same year but at 1.211 yr^{-1} (Fig. 5B). In only 1990 and 1992 did the SSM estimate a larger total instantaneous mortality rate than the SCA model, by 3% and 6%, respectively. The average total instantaneous mortality rate was 0.54 yr^{-1} in the SSM and 0.64 yr^{-1} in the SCA. The SSM estimated a yearly instantaneous trap net fishing mortality rate 15-54% lower than the SCA model. The yearly instantaneous gill net fishing mortality rate in the SSM ranged from 49% larger to 57% lower than the SCA model, though it was lower for most of the time series (24 out of 32 years). Time-invariant instantaneous natural mortality rate was approximately the same in both models- 0.190 ± 0.018 yr^{-1} and 0.184 ± 0.017 yr^{-1} in the SSM and SCA, respectively.

In the SSM the catchabilities provide estimates of the age- and year- specific proportionality between instantaneous fishing mortality rates and fishing effort. These fishery-specific relationships are presented in two ways- as catchability over years for each age (Figs. 6B, 6D) and as catchability over ages for each year, but normalized so that the maximum value is 1, as is typical for selectivity (Figs. 7B, 7D). The estimated degree of correlation in the AR(1) random walk for catchability (± 95% confidence intervals) was 0.843 ± 0.050 for the trap net fishery and 0.914 ± 0.036 for the gill net fishery (Table 3). For the SCA, the product of year-specific catchability and age- and year- specific selectivity has the same meaning as SSM catchabilities. We calculated these derived age- and year- specific catchabilities for the SCA and present them in the same way to compare how models quantify the relationship between fishing mortality and fishing effort (Figs. 6A, 6C, 7A, 7C).

Catchability at age was lower later in the time series than near the beginning across both models and both fisheries, but there were some marked differences in patterns between SSM and SCA (Fig. 6). Catchability of the gill net fishery steadily declined after 1995 in the SSM but peaked mid-way through the time series, in 2001, in the SCA (contrast Figs. 6A and 6B). Catchability of the trap net fishery had similar trends for both models, with peaks occurring in in 1994 and 2004-2006 for both the SCA and SSM (contrast Figs. 6C and 6D). The selectivity for both fisheries was dome shaped in the SSM, and largely asymptotic in the SCA (Fig. 7). The one notable deviation from this pattern was the gill net fishery in the SCA model, where some dome-like patterns occurred in the initial 10 years of the time series with a modest decline in selectivity at older ages. This pattern can be explained because selectivity in the SCA model was a function of mean length at age, and because fish got smaller on average through the time series, the old fish were as small late in the time series as the young highly selected fish earlier in the time series. In general, selectivity peaked at younger ages earlier in the time series for both models and both fisheries, and the age of full selectivity became progressively older in later years.

Management reference points differed between the SCA and SSM though not to the extent that differences in recommended harvest limits would have differentially impinged on fishery operations. In the last three years of the SCA and SSM assessments, the maximum (over ages) annual total mortality was 31% and 25%, and the SPR based on these mortality rates was 0.53 and 0.63, respectively. Thus, mortality rates were estimated to be below 65% and SPR above 0.2. In short, harvest limits based on either assessment would correspond to higher than status quo levels of fishing mortality.

Residuals for the fit to log scale total catch for both fisheries and both models were centered on zero, approximately normal, and generally did not trend through time, although the residuals for catch from the SSM model did exhibit more skew than the SCA model (Figs. B1-B3, C2-C4). Residuals for the age compositions for both fleets from the SCA model were patterned for several cohorts, especially in the first half of the time series (Figs. B4-B5). In the SSM model, the model overestimated the proportion of older ages in the trap net fishery and underestimated the proportion of individuals in the gill net fishery at the beginning of the time series, but the cohort effects were generally resolved relative to the SCA model (Figs. C5-C6). Both models exhibited retrospective bias in recruitment, though not spawning stock biomass (Figs. B6-B7, C7-C8). The Mohn's rho for recruitment was 0.989 for the SCA and 0.448 for the SSM, which both suggest a systemic bias in recruitment, though less so in the SSM. The Mohn's rho for spawning stock biomass was marginally larger and in the opposite direction in the SSM model (0.092) compared to the SCA (-0.038). The retrospective bias on SSB was within the acceptable range of -0.22 to 0.3 suggested for short lived species (Hurtado-ferro et al., 2015).

Sensitivity tests demonstrated that fixing the standard deviation of the lognormal distribution of the total catch at values 50% above or below the baseline did not change most estimated fixed effect parameters by more than 1.5% (Table 5). The estimated standard deviation of the trap net and gill net catchability process variability did decrease by 2.5% and 8% respectively, when the observation error was increased, suggesting a tradeoff between these values. For a full description of the model diagnostics of SSM, including time series of one step ahead (OSA) residuals and retrospective analyses, see Appendix C.

4. Discussion

This work demonstrates the feasibility of applying a state-space stock assessment model (SSM) with age-specific catchability as a state variable akin to year- and age- specific fishing mortality in previous applications (Berg and Nielsen, 2016; Nielsen and Berg, 2014). This also confirms the possibility of applying SSM in cases where there are no fisheries independent indices of abundance. To capitalize on state-space modeling's capacity to estimate several sources of process variability, the existing SCA model had to be re-parameterized such that recruitment and age-specific catchability were random walk processes. Merely specifying that yearly variability in catchability, recruitment, or selectivity were random effects, without changing the parameterization of the SCA model resulted in model non-convergence.

These necessary changes to the process model parameterization, though increasing realism and model flexibility, inevitably led to changes in model output that cannot be parsed from changes due only to converting a statistical catch at age model (SCA) to an SSM. Some changes in output, like trends in abundance and fishing mortality, were minimal. Others, like recruitment in the latter part of the time series, and the catchability and selectivity patterns, substantially altered the interpretation of population and fisheries dynamics.

Estimates of time-varying recruitment from the SSM exhibited less interannual variation and less difference between the maximum and minimum value than the SCA model, which reflects autocorrelation in the random walk process (Thorson et al., 2014). During much of the assessment, recruitment can be strongly informed by how a cohort was represented in subsequent years of catch data which is why estimates at the end of the assessment period are generally the most uncertain (Brooks and Legault, 2016). In the absence of future information, the SCA model was guided by the explicit relationship between recruitment and spawning stock biomass (SSB) in past years while SSM, lacking such a function, remained largely the same in the final 5 years (Fig. 3B). This lack of information at the end of the time series may have driven the retrospective bias in recruitment observed in the SSM model. Though state-space models are expected to exhibit less retrospective patterns than non-state-space models and the SSM did have a lower Mohn's rho statistic than the SCA for recruitment, the value was still within the range that would suggest systemic bias, likely owing to the recruitment parameterization, rather than the integrated likelihood (Hurtado-ferro et al., 2015; Perreault et al., 2020; Stock et al., 2021). The pattern of negative residuals from 1996-2005 in the trap net fishery and 1994-2007 in the gill net fishery also suggests that recruitment may have been overestimated in the middle of the time series. This is also likely due to the random walk parameterization and values constrained to remain high so the model could predict the very high recruitment in 1995 and 2005. When designing state-space models stock assessment models and interpreting the results for management, careful consideration should be given to the amount of structure or flexibility afforded the recruitment process because extreme low or high recruitment events can influence the estimates of previous and subsequent years if there is intra-year correlation. Ideally, the Lake Michigan lake whitefish model should have enough flexibility to account for the relationship between recruitment and SSB while also incorporating how ecosystem changes like ice cover, prey availability, and habitat degradation due to dreissenid invasion may create additional yearly variability (Ebener et al., 2021). The solution may lie in one or several alternative recruitment structures including 1) parameterizing variable parameters of the stock recruitment curve, 2) employing more dynamic autocorrelation processes with time series models that estimate how much to "remember" from previous years (e.g., AR(1)), or 3) utilizing a "mixture-distribution" of two distributions controlled via a Bernoulli distribution that accommodates occasional spikes or dips in recruitment (Johnson et al., 2016; Maunder and Thorson, 2018; Thorson et al., 2014).

The SSM estimated dome-shaped selectivity for both fisheries, so it predicted older (and thus larger) individuals were present but less vulnerable to capture. The SCA was constrained to fit an asymptotic selectivity curve for the trap net fishery such that the oldest fish were catchable at a comparable rate to middle-aged fish. An asymptote was estimated for most years for the gill net fishery as well. Sensitivity tests of the SSM which forced an asymptote for the trap net fishery confirmed that differences in the estimated selectivity curve drove the differences in abundance, and by extension, spawning stock biomass. Both asymptotic and dome-shaped selectivity have been previously reported for trap net gear and either relationship could be reasonably expected for Lake Michigan lake whitefish in WFM-03 (Dunlop et al., 2018; Hansen et al., 2008; Jeong et al., 2000). The SSM had limited data to inform selectivity because the average age of lake whitefish in this region is lower than in adjacent regions and older ages were not strongly represented in the harvest (Caroffino and Seider, 2020). This flexibility to estimate time-varying selectivity without specifying an explicit and somewhat arbitrary function, is a hallmark of state-space stock assessment models (Nielsen et al., 2021). However, if there is good reason to specify or restrain it, there are several future options to do so. The functional form could be implemented as a "prior" about which penalties are assessed, rather than requiring an exact match. This approach could be implemented with the selectivity parameters fixed, changing gradually over time (perhaps by an autoregressive process), or changing at discrete time blocks (Cronin-fine and Punt, 2021; Martell and Stewart, 2014; Stock and Miller, 2021). Future lake whitefish assessments might consider a thorough model selection and review procedure, with dome-shaped selectivity for the trap net fishery included as a possible interpretation of fishery dynamics.

The simultaneous estimation of observation and process error variances is a touted hallmark of state-space modeling, but was not realized in this model. This inability to estimate the observation error variance within the model may be caused by the estimation of variance of time varying catchability. Sensitivity tests demonstrated a tradeoff between observation error standard deviation, σ_{CG}, and catchability standard deviation, σ_G, because when the former was fixed at a higher value, the latter was estimated at a lower value. The observation error standard deviation may have been estimable in this model if there were greater contrast in fishing mortality and catch over time, or if there were informative survey data. Observation error standard deviation can be approximated from the observed data, so estimating the standard deviation of catchability, an unobservable state variable, was prioritized in this model, a practice also used by others (Francis, 2011). The age composition data were fit using a multinomial distribution for which the effective sample sizes were specified *a priori*. Efforts to calculate effective sample sizes through established iterative reweighting techniques led to data overweighting (i.e. the effective sample sizes were orders of magnitude *larger* than observed sample size), fitting the age proportion data precisely at the expense of high process model variability (Francis, 2011; Truesdell et al., 2017). The total catch data were fit using a log-normal distribution but trying to estimate the standard deviation resulted in model non-convergence. Estimability of observation error variance may be beyond the upper limits of model flexibility for this SSM given the process model parameterization and data availability. Limitations on estimating the observation error variance have not been evident in other state-space models that included index data and assumed constant catchability (Nielsen and Berg, 2014; Perreault et al., 2020). Future research could investigate the reasons for this difference. In particular, it is an open question whether estimation of observation error variance and time varying catchability is possible with different distributions of the catch data (e.g., Dirichlet multinomial for proportions at age or a multivariate log normal for catch at age (Nielsen and Berg, 2014; Thorson et al., 2017) or if provision of external estimates of observation error variance is a fundamental requirement when allowing time-varying catchability. If it is a fundamental property, providing external estimates of observation error variance in order to allow for time-varying fishery catchability seems preferable.

Though fisheries-dependent sampling is non-random and prone to bias, its continued use may be justified by its extensive availability, inexpensiveness, and the capabilities of modern assessment models to account for violations of the typical assumption of proportionality with abundance. This state-space stock assessment model uses variability in the proportionality coefficient, catchability, to account for a stochastic relationship between CPUE and abundance across age and time, combatting the concerns of hyperstability or hyperdepletion that surround the use of effort data (Rose and Kulka, 1999). Other research has explored standardization methods using generalized linear models (GLM) or generalized additive models (GAM) to explain how factors like area, time, and gear can influence the relationship between abundance and CPUE in a non-linear fashion (Deroba and Bence, 2009; Ducharme-Barth et al., 2022; Grüss et al., 2019). Specific covariates such as season, sampling depth, or hook and bait characteristics can be directly included in the model to explain variation in catchability (Grüss et al., 2019; Johnson et al., 2019). Even with fine scale catch data and informative covariates, specifying catchability as a time-varying random effect can allow for temporal variability not explained by the covariates, without overfitting the model.

Use of this SSM in future cases may challenge preconceived assumptions about population or fishery dynamics that were assumed impossible, unrealistic, or inestimable given the available data and limits to parameterization. The SSM structure easily lends itself to estimating process variation in natural mortality, selectivity, abundance, and many other factors previously assumed to be invariant or fixed. This research demonstrated that a lack of fisheries independent indices is not a hurdle to employing SSM. Many more fisheries may consider this approach a viable option, maintaining that there is sufficient informative effort data to relate catchability to fishing mortality. Highly migratory species like tunas, billfish, and sharks, data-poor species like elasmobranchs, deep sea fisheries, and developing fisheries are examples of those that have limited to no fisheries independent data, or the continued collection of such data may not be cost effective and may therefore benefit from this SSM approach (Costello et al., 2012; Dennis et al., 2015; Langley et al., 2009; Lynch et al., 2018; Victorero et al., 2018). Several Great Lakes stocks which have been previously assessed using a penalized likelihood statistical catch-at-age model may also be candidates for fitting a state-space stock assessment model, especially one such as this which can accommodate fisheries-dependent data. For example, yellow perch in Lake Michigan are assessed using recreational and commercial fisheries effort and time-varying catchability, though these models include informative fisheries-independent data (Wilberg et al., 2005). As another example, Chinook salmon stocks in Lakes Michigan and Huron lack reliable survey information and abundance is estimated entirely with catch and effort data (Brenden et al., 2012; Clark et al., 2016). Likewise, consideration of fishery dependent CPUE information has been suggested for use alongside fishery independent information when stakeholder perceptions of stock status are inconsistent with a stock assessment, as in Gulf of Maine and Georges Bank Cod (NEFSC, 2022). While a lack of fishery independent data may create new challenges, such as the inability to estimate observation error variance, they are not insurmountable, and many benefits of state-space modelling can still be achieved.

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Appendix A. Description of data collection and processing prior to inclusion in age-based stock assessment models.

Fishery and biological data of lake trout and lake whitefish have been collected in the 1836 Treaty waters of the Great Lakes since 1985, though the time series for some regions begins later. Each year, the time series up to but *not* including that year are used to build stock assessments that are used to make harvest recommendations for the following year (i.e., the time series 1986-2017 is used in a model built in 2018 that makes recommendations for 2019). A catch reporting system provides monthly total harvest, $H_{y,G}$, in weight, and effort data, $E_{y,G}$, in lifts for the trap net fishery, or length of net for the gill net fishery from 1986 to 2017, which are pooled from daily reports mandated for each licensed commercial fisher (Ebener et al., 2005). Biological data were collected opportunistically by sampling catch from commercial trap and gill net fisheries from 1986-2017. The number of individual fish sampled each year varied considerably over time and between fisheries, from 86-1261 in the trap net fishery and 0-716 in the gill net fishery (Fig. A1).

In general, aging was done using scale samples for smaller (and presumably younger) fish and otoliths for larger (and presumably older) fish. A total of 2,484 scale samples were taken from individuals ranging from 375-669mm (averaging 464mm), and a total of 748 otolith samples were collected, from individuals ranging from 430-623mm (averaging 523mm). Otoliths are a more accurate and precise aging tool than either fin rays or scales to age lake whitefish and were assumed to be unbiased measurements (Herbst and Marsden, 2011). Because scale samples yield similar age estimates as otoliths at younger ages but are less precise at older ages, dividing the aging between the two structures should minimize aging error (Herbst and Marsden, 2011). Weight at age, $W_{a,y}^{(harv)}$, and length at age, $L_{a,y}$, for the harvest in each year was determined using a growth model with year- and cohort- specific parameters, using data from both fisheries (He and Bence, 2007). These calculations were done prior to assessment model fitting and provided as inputs to the assessment model. Weight at age from the sampled harvest and samples from a graded-mesh gill net survey were used to calculate population weight at age at the beginning of the year, $W_{a,y}^{(init)}$, and at the time of spawning, $W_{a,y}^{(spawn)}$, assuming that harvest occurs on June 30th, spawning occurs on October 30th, and growth from one year to the next follows an exponential model.

The total harvest in weight by year and fishery, $H_{y,G}$, was converted into total harvest in numbers using the average weight by year and fishery, $\overline{W}_{y,G}$. The observed total catch in each year by each fishery $C_{y,G}$ was a function of total harvest, the mean weight, and a year- and fishery- specific adjustment term, $A_{y,G}$, that corrected for under reporting of each fishery,

$$C_{y,G} = \frac{\frac{H_{y,G}}{\overline{W}_{y,G}}}{A_{y,G}}.$$

Underreporting rate was estimated as the ratio of reported whitefish harvested by the fishers to the reported whitefish purchased by wholesalers (Ebener et al., 2005). Observed proportions at age for each fishery and year, $P_{a,y,G}$ were calculated from the commercial sampling data, by normalizing the number sampled at age and year by the total sampled in each year. Only fish age 4 and older were included in the stock (younger fish were extremely rarely caught) and all fish age 15 and older were aggregated into a plus group. The oldest recorded age was 32, however, individuals aged 20 or older were exceedingly rare in this region (<0.1% of sampled individuals).

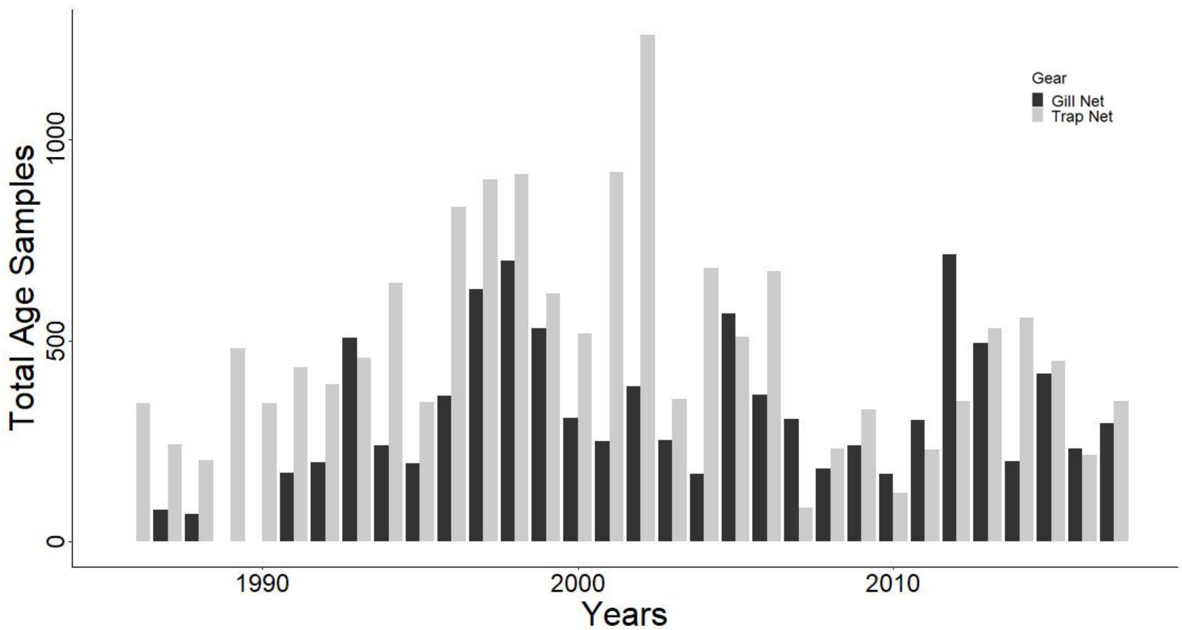

Fig. A1: Number of fish sampled and aged from the gill net and trap net fishery of Lake Michigan lake whitefish in region WFM-03 from 1986-2017.

Appendix B. Description of current statistical catch at age model (SCA) used to assess Lake Michigan lake whitefish and parameter estimates.

We refer to this model as the current assessment, despite some minor modifications that occurred to the model in 2021, and it is an age-based statistical catch at age model (henceforth "SCA") fit to commercial trap net and gill net fishery data with additional data inputs described below (Caroffino and Seider, 2020; Ebener et al., 2005; Truesdell and Bence, 2016). The model was built using AD Model Builder (Fournier et al., 2012). The years of data used in the assessment were from 1986 to 2017 (i.e., y = 1986, 1989 … 2017), the age classes ranged from 4 to 15+ (i.e., a= 4, 5, … A, where A=15+), and there were catch and effort data for each of the two fisheries (i.e., G=g, t).

The model estimated the abundance of individuals ages 4-9 in 1986 and the abundance (i.e., recruitment) of age 4 individuals in each year. Log-scale recruitment was calculated as the sum of two log-scale parameters- an average recruitment, $\bar{R}$, and a vector of deviations, D_y,

$$\log N_{4,y} = \log \bar{R} + \log D_y.$$

The number of individuals from age 4 to 9 in the initial year were calculated in a similar way, using the same average recruitment and another set of deviation values d_a,

$$\log N_{a,1986} = \log \bar{R} + \log d_a \text{ where } a < 10.$$

The number of individuals in the initial year from age 10 to 15 were set to 0, because few or no fish of these ages were detected in the catch and there were insufficient data to reliably inform abundance and catchability. The effects of this simplification on model output, particularly in later years of the time series, are likely negligible. The vectors of D_y and d_a were constrained to collectively sum to 0. All other abundances at age and year, after the initial year and initial age, $N_{a,y}$, followed an exponential decay with all fish age A or older subject to the same year-specific instantaneous mortality (Table 2, Eq. 1.4). The instantaneous total mortality at age and year, $Z_{a,y}$, was the sum of age-, year-, and fishery- specific instantaneous fishing mortality, $F_{a,y,G}$, and a single estimated instantaneous natural mortality, M (Eq. 1.5). Instantaneous fishing mortality was the product of year- and fishery- specific catchability, $q_{y,G}$, year- and fishery- specific fishing effort, $E_{y,G}$, and age- and year- and fishery- specific selectivity, $s_{a,y,G}$ (Eq. 1.6a). Log-scale catchability varied over time according to a random walk (Eq. 1.7a).

Selectivity at age for each fishery was a function of mean length at age and varied over time in the trap net fishery. The selectivity of the trap net fishery was modeled as a logistic function of mean length at age each year, normalized against a reference length, 455 mm (i.e., selectivity was 1.0 at this mean length at age):

$$s_{a,y,t} = \frac{\frac{1}{1+\exp(-p_{2,t}(L_{y,a}-p_{1,y,t}))}}{\frac{1}{1+\exp(-p_{2,t}(455-p_{1,y,t}))}}$$

$$\log p_{1,y+1,t} = \log p_{1,y,t} + \varepsilon_y^{(s)};\ \varepsilon_y^{(s)} \sim N(0, \sigma_s^2\ ); y < 2017.$$

The parameters, $p_{1,y,t}$ and $p_{2,t}$, are the inflection point (varying over years), and the determinant of the slope at the inflection point (constant over years), respectively. The inflection point for the initial year was estimated and then varied over according to a random walk, the distribution of which was included in the total objective function (Eq. 3.4),

Selectivity of the gill net fishery used a lognormal function with two estimated parameters, $p_{1,g}$ and $p_{2,g}$, and was normalized to equal 1.0 for a mean length at age of $\exp(p_{2,g})$,

$$s_{a,y,g} = \frac{\frac{1}{\sqrt{2\pi}p_{1,g}L_{y,a}} * \exp(\frac{-(\log L_{y,a}-p_{2,g})^2}{2p_{1,g}^2})}{\frac{1}{\sqrt{2\pi}p_{1,g}\exp p_{2,g}}}.$$

Spawning stock biomass, $B_y^{(Spawn)}$, in each year was calculated by multiplying the weight at age during spawning (adjusted with maturity schedule), by the number of individuals at age in each year (Eq. 1.8).

The predicted age-, year-, and fishery- specific catch, $C_{a,y,G}$, was calculated from the Baranov catch equation (Eq. 2.1). The annual proportions at age were calculated from the age- and year- specific total catch (Eq. 2.2). The objective function of the SCA model, *T*, was the sum of the negative log prior probability density of the parameters, NLP, and the negative log likelihood of the data given the parameters, NLL (Eq. 3.1). The NLP was the sum of explicit components explaining variability in recruitment, $N_{4,y}$, log-scale catchability (trap and gill net), and selectivity (trap net). Priors for all other parameters were from uniform distributions, specified via bounds for the parameters.

Recruitment was constrained such that estimated values did not deviate substantially from a mean predicted by a Ricker stock recruitment function, $\widehat{N}_{4,y}$ which depended on Ricker stock recruitment parameters, α and β, and year-specific spawning stock size in eggs, ϵ_y

$$\log \widehat{N}_{4,y+5} = \alpha \epsilon_y^{(-\beta \epsilon_y)}.$$

The predicted value was compared to the current estimates, $N_{a,y}$, using a likelihood framework during model fitting (Eq. 3.2a). Fecundity data, including age- and year- specific maturity, $m_{a,y}$, the average number of eggs per kilogram, e, and the average proportion of females in the spawning population, f, were input into the model. The maturity matrix was a 5-year running average that was the same across all 1836 treaty waters and calculated by applying an age/length key to maturity at length data. Eggs per kilogram was also a universal value based on samples collected in 1983 and 1996 (Ebener et al., 2005). The proportion of females was calculated from samples of the commercial harvest and was a single age- and year-invariant value for each management unit, which was 0.4845 for WFM-03 (Ebener et al., 2005; Patriarche, 1977).

Spawning stock size (i.e., eggs) was calculated from maturity at age, weight at age during spawning, $W_{y,i}^{(spawn)}$, eggs per kilogram, percent female, numbers at age, and total instantaneous mortality for the proportion of the year that occurs before spawning (0.838),

$$\epsilon_y = \sum_{i=4}^{A} m_{y,i} W_{y,i}^{(spawn)} ef N_{i,y}^{-Z_{y,i}*0.838}$$

The deviations from predicted mean recruitment were assumed to be log normally distributed (Eq. 3.2a). Note that these terms start in 1991, which is the year class produced by the spawning biomass in 1986 (the first year being modeled). The errors for the log-scale trap net and gill net catchability random walks were assumed to come from fishery-specific normal distributions (Eq. 3.3a). Similarly, the errors for the random walk of the time-varying trap net selectivity parameter, $p_{1,y,t}$, were assumed to come from a normal distribution (Eq. 3.4). The NLP also included a prior expectation on instantaneous natural mortality, that it was assumed to arise from a log normal distribution with median $M = 0.2$ and standard deviation, $\sigma_M = 0.1$ (Eq. 3.5a).

The NLL included four summed components, for the total catch and proportions at age of the trap net and gill net fisheries. The observed total catch by year, for each fishery was assumed to come from a log normal distribution, with median equal to the predicted catch (Eq. 3.6). The observed catch proportions at age by year for each fishery were assumed to behave as though they resulted from sampled numbers at age following a multinomial distribution, with fishery-specific effective sample size, n_G determined *a priori* using an iterative reweighting algorithm (Francis, 2011; Truesdell et al., 2017) (Eq. 3.7). The effective sample size in each year was the product of the number of fish sampled and the gear-specific scalar, 0.12 and 0.06 for the trap and gill net fisheries, respectively, rounded to the nearest whole number. Those effective sample sizes are reported in Table B1.

The standard deviations for the above distributions were calculated as the product of a single common standard deviation term, σ, which was estimated, and a standard deviation specific multiplier, φ, that was pre-specified. This constraint was implemented because in this model structure there was insufficient information to independently estimate the standard deviations of each process variability and observation error distribution. The model used a minimization algorithm to determine the point estimates for parameters that minimized the total objective value T. The estimated parameters and standard errors are reported in Table B2.

Several plots are included to illustrate model diagnostics. Histogram plots of ordinary least squared (OLS) residuals (observed-expected value) of (A) total trap net catch on the log-scale, (B) total gill net catch on the log-scale, and one step ahead (OSA) residuals of (C) trap net proportions at age, and (D) gill net proportions at age are reported in Fig. B1. The OLS residuals of the total trap net and gill net fishery catch over time are reported in Figs. B2-B3. The OSA residuals of proportions at age are plotted as a bubble plot to highlight potential patterns across age and time (Figs. B4-B5). Retrospective plots for the recruitment and spawning stock biomass are reported in Figs. B6-B7.

Table B1. Year-specific effective sample size of the multinomial distribution of proportion at age of the trap net, n_t, and gill net, n_g, fisheries

Year	n_t	n_g
1986	40	0
1987	28	5
1988	24	4
1989	56	0
1990	40	0

1991	51	10
1992	46	12
1992	53	30
1993	75	14
1994	40	11
1995	97	21
1996	105	37
1997	107	41
1998	72	31
1999	60	18
2000	107	15
2001	147	23
2002	41	15
2003	79	10
2004	59	33
2005	78	21
2006	10	18
2007	27	11
2008	38	14
2009	14	10
2010	27	18
2011	41	42
2012	61	29
2013	65	12
2014	52	24
2015	25	13
2016	41	17
2017	40	0

Table B2. Parameter estimates and standard error of SCA model

Parameter (Symbol)	Estimate	Standard Error
M	0.1838	0.0171
σ	0.0445	0.0026
$q_{1986,t}$	0.0221	0.0051
$q_{1987,t}$	0.0275	0.0055
$q_{1988,t}$	0.0287	0.0047
$q_{1989,t}$	0.0241	0.0040
$q_{1990,t}$	0.0208	0.0035
$q_{1991,t}$	0.0270	0.0042
$q_{1992,t}$	0.0278	0.0040
$q_{1993,t}$	0.0302	0.0044
$q_{1994,t}$	0.0334	0.0048

$q_{1995,t}$	0.0328	0.0051
$q_{1996,t}$	0.0317	0.0048
$q_{1997,t}$	0.0303	0.0047
$q_{1998,t}$	0.0281	0.0043
$q_{1999,t}$	0.0286	0.0038
$q_{2000,t}$	0.0254	0.0037
$q_{2001,t}$	0.0220	0.0029
$q_{2002,t}$	0.0188	0.0029
$q_{2003,t}$	0.0206	0.0032
$q_{2004,t}$	0.0280	0.0041
$q_{2005,t}$	0.0258	0.0039
$q_{2006,t}$	0.0247	0.0036
$q_{2007,t}$	0.0235	0.0039
$q_{2008,t}$	0.0189	0.0028
$q_{2009,t}$	0.0164	0.0023
$q_{2010,t}$	0.0142	0.0022
$q_{2011,t}$	0.0155	0.0025
$q_{2012,t}$	0.0147	0.0025
$q_{2013,t}$	0.0116	0.0023
$q_{2014,t}$	0.0093	0.0022
$q_{2015,t}$	0.0080	0.0023
$q_{2016,t}$	0.0064	0.0022
$q_{2017,t}$	0.0067	0.0025
$q_{1986,g}$	0.1015	0.0147
$q_{1987,g}$	0.0858	0.0114
$q_{1988,g}$	0.0809	0.0103
$q_{1989,g}$	0.0811	0.0112
$q_{1990,g}$	0.0486	0.0059
$q_{1991,g}$	0.0687	0.0086
$q_{1992,g}$	0.0608	0.0067
$q_{1993,g}$	0.0682	0.0084
$q_{1994,g}$	0.0614	0.0081
$q_{1995,g}$	0.0659	0.0086
$q_{1996,g}$	0.0484	0.0064
$q_{1997,g}$	0.0525	0.0075
$q_{1998,g}$	0.0454	0.0063
$q_{1999,g}$	0.0389	0.0052
$q_{2000,g}$	0.0486	0.0070
$q_{2001,g}$	0.1061	0.0167
$q_{2002,g}$	0.0734	0.0113
$q_{2003,g}$	0.0435	0.0066
$q_{2004,g}$	0.0631	0.0101
$q_{2005,g}$	0.0656	0.0104
$q_{2006,g}$	0.0754	0.0120
$q_{2007,g}$	0.0701	0.0122

$q_{2008,g}$	0.0743	0.0118
$q_{2009,g}$	0.0532	0.0073
$q_{2010,g}$	0.0448	0.0060
$q_{2011,g}$	0.0555	0.0084
$q_{2012,g}$	0.0435	0.0072
$q_{2013,g}$	0.0329	0.0066
$q_{2014,g}$	0.0509	0.0125
$q_{2015,g}$	0.0257	0.0070
$q_{2016,g}$	0.0303	0.0088
$q_{2017,g}$	0.0198	0.0063
$p_{1,1986,t}$	475.38	9.5069
$p_{1,1987,t}$	483	8.735
$p_{1,1988,t}$	475.83	10.337
$p_{1,1989,t}$	471.67	7.9452
$p_{1,1990,t}$	479.03	10.072
$p_{1,1991,t}$	463.82	8.2848
$p_{1,1992,t}$	466.99	6.9187
$p_{1,1993,t}$	470.45	6.5829
$p_{1,1994,t}$	467.32	6.5738
$p_{1,1995,t}$	479.12	5.7553
$p_{1,1996,t}$	480.74	5.4075
$p_{1,1997,t}$	478.89	5.1605
$p_{1,1998,t}$	491.21	5.3963
$p_{1,1999,t}$	470.89	6.7586
$p_{1,2000,t}$	473.77	6.4606
$p_{1,2001,t}$	447.77	5.9078
$p_{1,2002,t}$	473.12	5.6466
$p_{1,2003,t}$	472.59	7.4029
$p_{1,2004,t}$	458.43	6.8059
$p_{1,2005,t}$	461	8.519
$p_{1,2006,t}$	437.27	7.8146
$p_{1,2007,t}$	435	8.3108
$p_{1,2008,t}$	435.06	7.9925
$p_{1,2009,t}$	450.69	6.734
$p_{1,2010,t}$	472.2	7.4435
$p_{1,2011,t}$	469.65	6.3439
$p_{1,2012,t}$	478.42	6.9458
$p_{1,2013,t}$	477.52	7.1065
$p_{1,2014,t}$	439.58	7.3909
$p_{1,2015,t}$	463.28	9.3819
$p_{1,2016,t}$	476.64	13.21
$p_{1,2017,t}$	478.23	11.348
$p_{2,t}$	0.0600	0.0040
$p_{1,g}$	0.0833	0.0063
$p_{2,g}$	6.29	0.0154

$\bar{R}$	504140	49815
D_{1986}	1.4627	0.2157
D_{1987}	0.8984	0.1619
D_{1988}	0.5004	0.1086
D_{1989}	0.6276	0.1224
D_{1990}	1.624	0.2177
D_{1991}	2.0457	0.2577
D_{1992}	2.3842	0.2723
D_{1993}	1.6725	0.2007
D_{1994}	1.3842	0.1679
D_{1995}	3.0649	0.2843
D_{1996}	2.5721	0.2435
D_{1997}	2.4709	0.2369
D_{1998}	2.2904	0.2348
D_{1999}	2.3116	0.2563
D_{2000}	2.0771	0.2498
D_{2001}	1.6651	0.2206
D_{2002}	1.5444	0.2248
D_{2003}	1.2869	0.2152
D_{2004}	2.1706	0.3452
D_{2005}	2.9389	0.4021
D_{2006}	2.4684	0.3507
D_{2007}	2.0104	0.2881
D_{2008}	1.657	0.2356
D_{2009}	1.4356	0.2023
D_{2010}	1.1113	0.1674
D_{2011}	0.9298	0.1522
D_{2012}	0.8216	0.1522
D_{2013}	0.8075	0.1805
D_{2014}	0.7559	0.1974
D_{2015}	0.9726	0.3089
D_{2016}	0.6199	0.2238
D_{2017}	0.6573	0.3222
d_5	1.006	0.1666
d_6	0.4012	0.0992
d_7	0.0923	0.0462
d_8	0.0242	0.0235
d_9	0.0134	0.0175
α	0.0003	0.0001
β	1.17E-10	3.64E-11

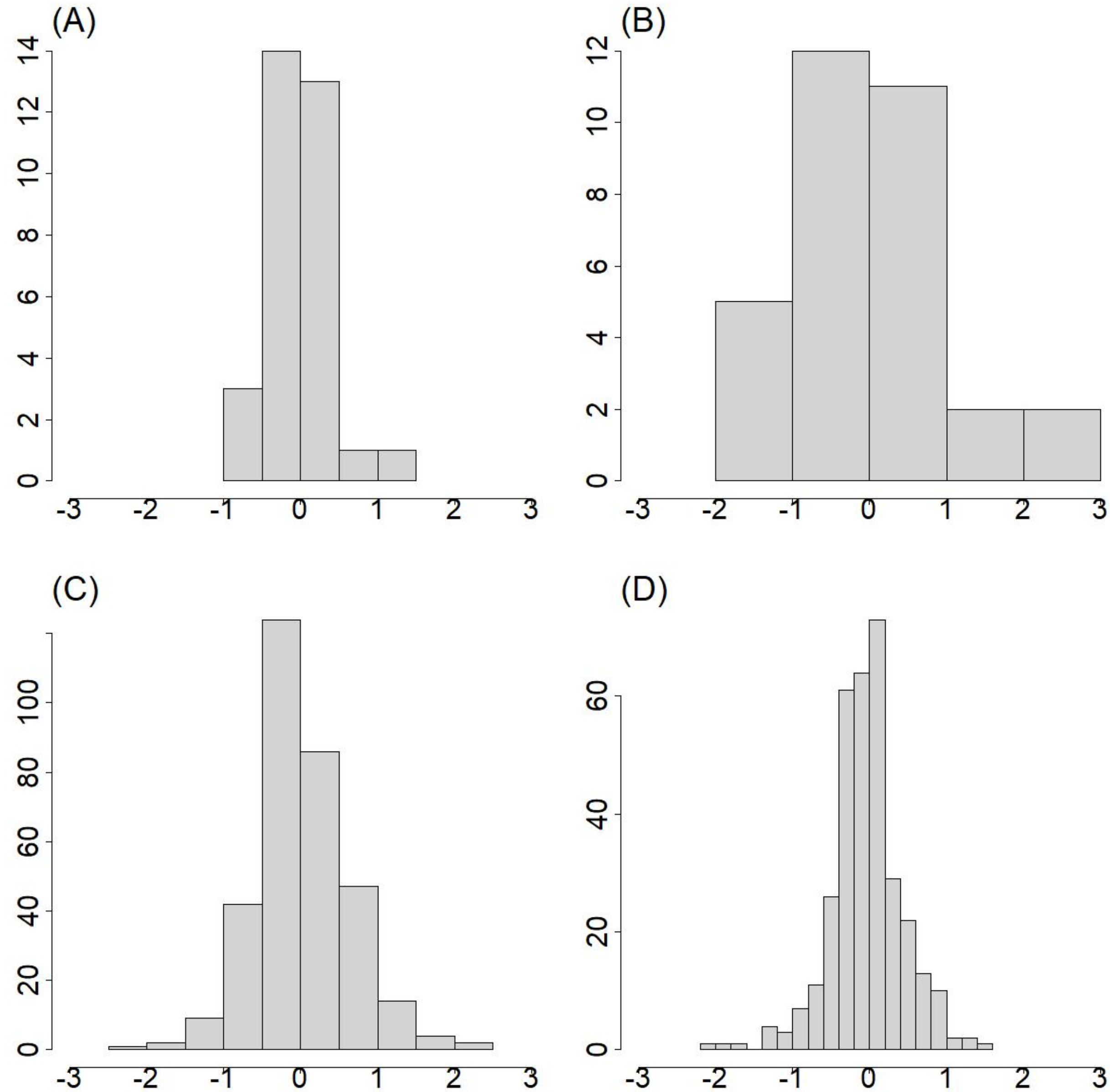

Fig. B1. Histogram plots of ordinary least squared (OLS) residuals of (A) total trap net catch on the log-scale and (B) total gill net catch on the log-scale, and one step ahead (OSA) residuals of (C) trap net proportions at age and (D) gill net proportions at age.

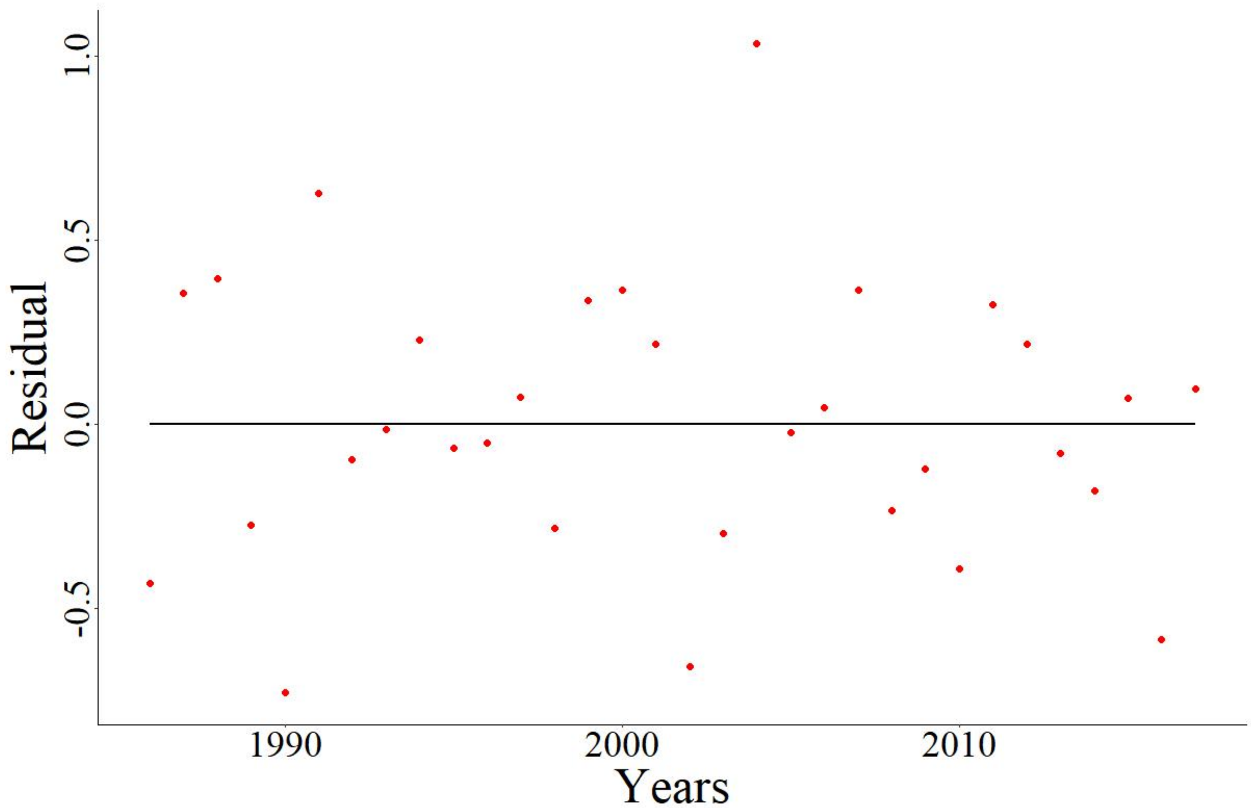

Fig. B2. Ordinary least squared (OLS) residuals of total log-scale catch of the trap net fishery over time. Observed catch was modeled as a lognormal distribution with mean equal to the expected catch and standard deviation 0.067.

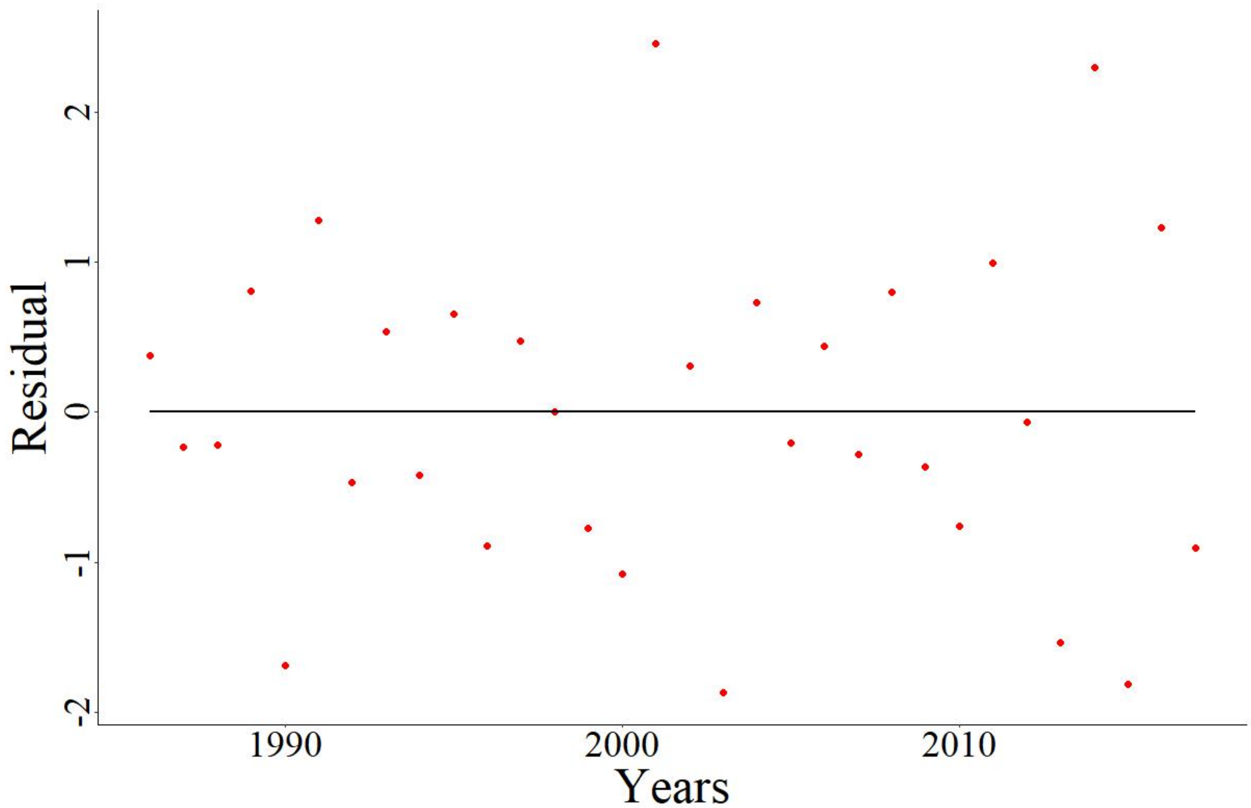

Fig. B3. Ordinary least squared (OLS) residuals of total log-scale catch of the gill net fishery by year. Observed catch was modeled as a lognormal distribution with mean equal to the expected catch and standard deviation 0.067.

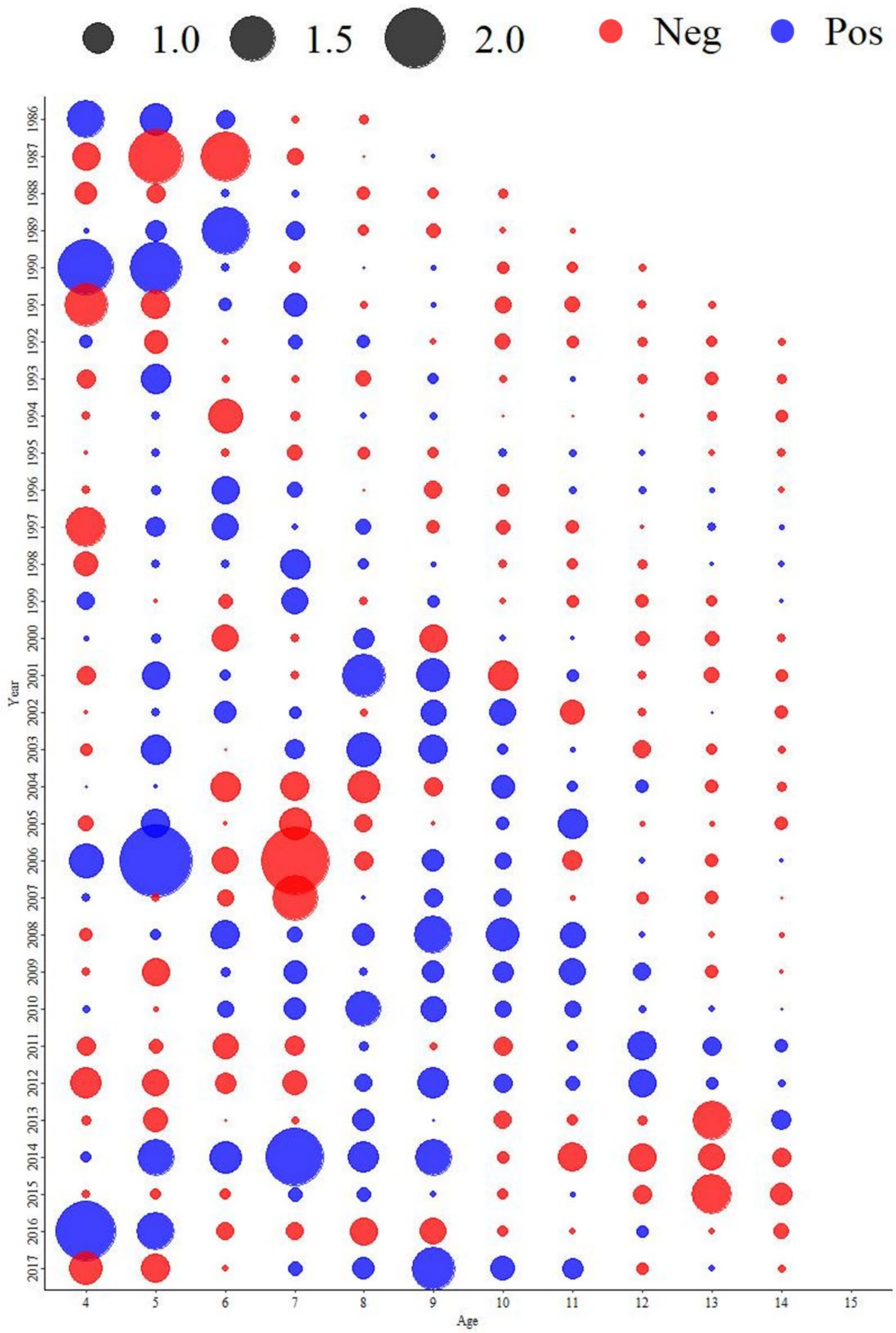

Fig. B4. One step ahead (OSA) residuals of proportions at age of the trap net fishery. Observed proportions were modeled as a multinomial distribution with year-specific effective sample size. No residuals were reported for year and age combination where the expected and observed value was 0 (older ages in the first 6 years) or for age 15+, because the way OSA residuals are calculated does not allow for estimates in the oldest age.

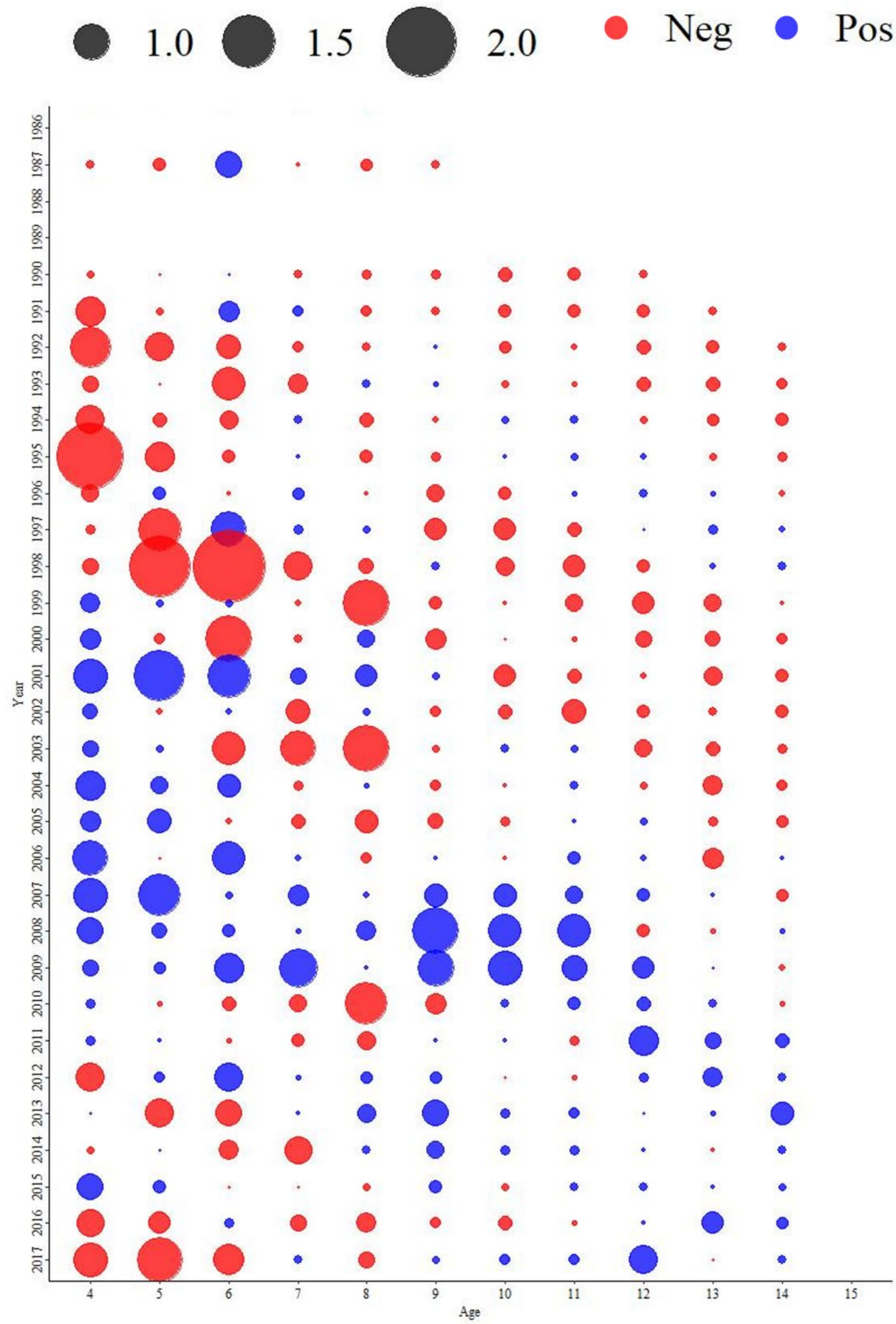

Fig. B5. One step ahead (OSA) residuals of proportions at age of the gill net fishery. Observed proportions were modeled as a multinomial distribution with year-specific effective sample size. No residuals were reported for year and age combination where the expected and observed value was 0 (older ages in the first 6 years) or for age 15+, because the way OSA residuals are calculated does not allow for estimates in the oldest age. Note that years 1986, 1989, and 1990 are also absent because the sample size was zero.

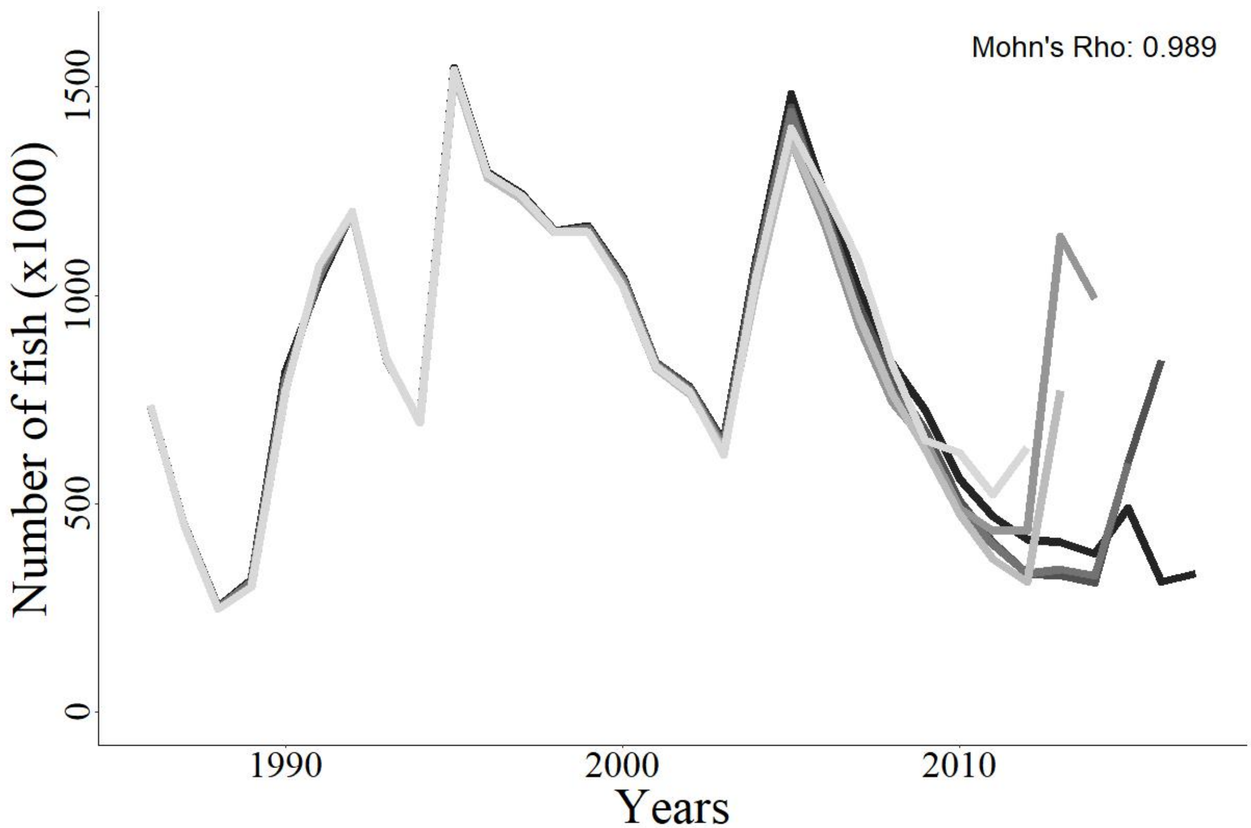

Fig. B6. Retrospective analysis of estimated recruitment. The SCA model was refit after removing sequential years of the most recent observations. Dark colors indicate more complete data sets and lighter colors indicate less complete data sets.

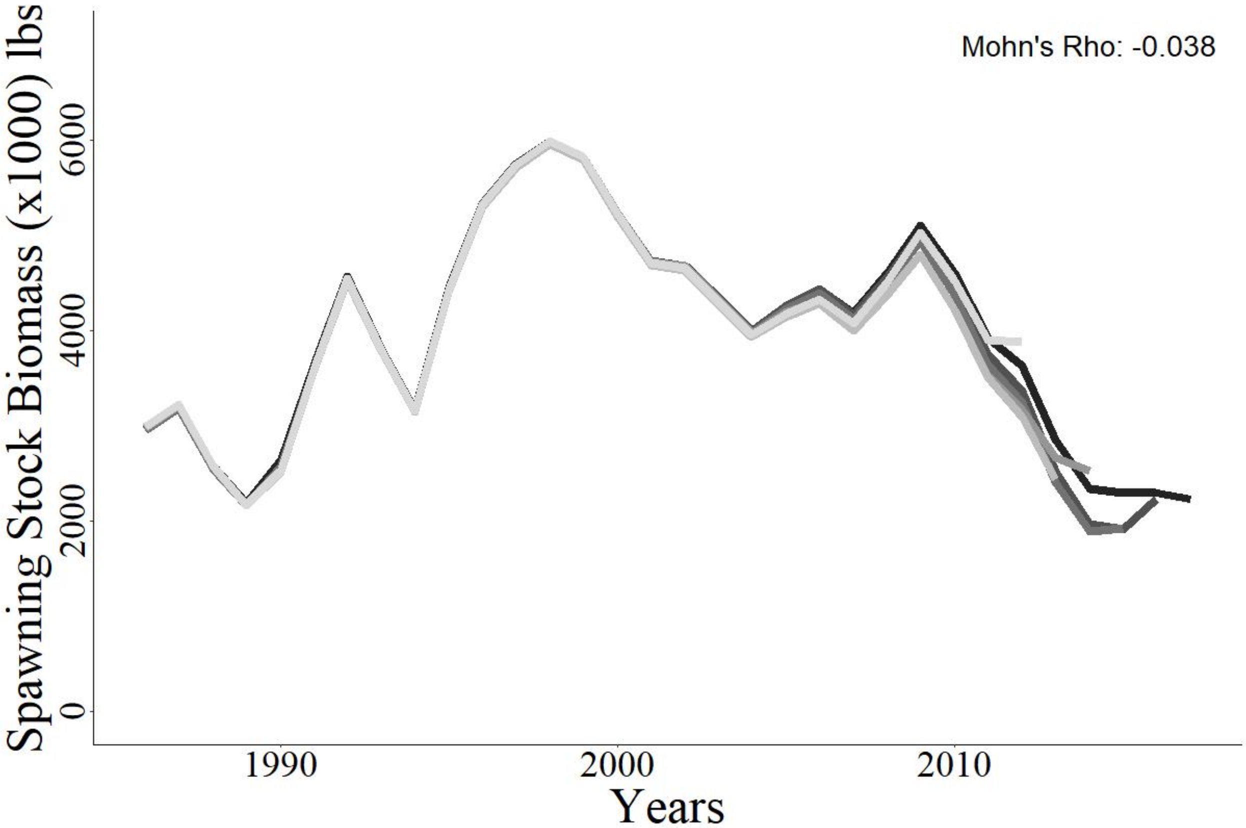

Fig. B7. Retrospective analysis of estimated spawning stock biomass. The SCA model was refit after removing sequential years of the most recent observations. Dark colors indicate more complete data sets and lighter colors indicate less complete data sets.

Appendix C. Model diagnostics and additional plots for the state-space model (SSM).

The state-space stock assessment model predicted temporally variability in age structure with older ages being more represented in the population in later years (Fig. C1). The state-space stock assessment model (SSM) fit the catch and catch composition data well for both fisheries with plots of the predicted and observed total harvest over time entirely overlapping, with no difference distinguishable through line graphs, and therefore are not reported here. The histograms of one step ahead (OSA) residuals for the total catch on the log-scale, proportions at age, and catchability process variability are plotted in Fig. C2. The residuals were plotted over time in Figs. C3-C6. Retrospective plots for the recruitment and spawning stock biomass are reported in Figs. C7-C8.

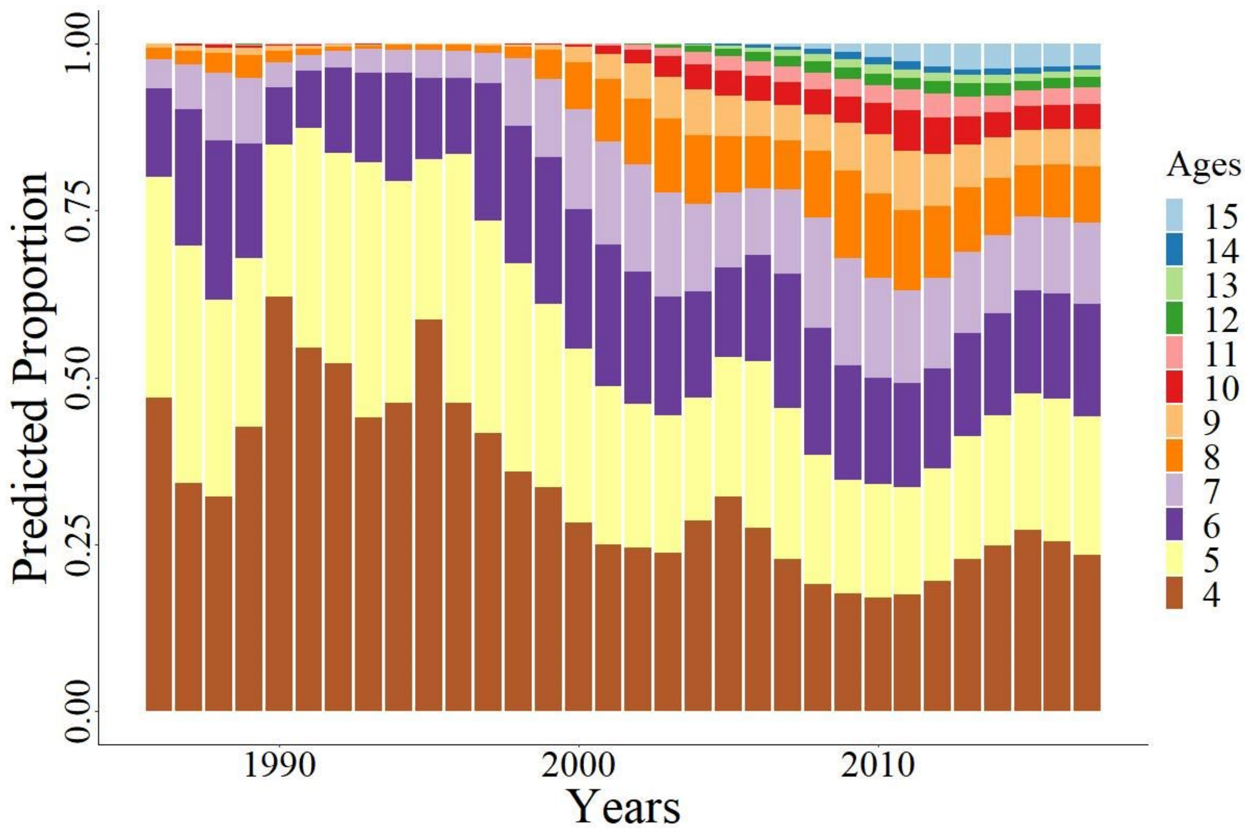

Fig. C1. Predicted proportions at age over time in the state-space stock assessment model (SSM).

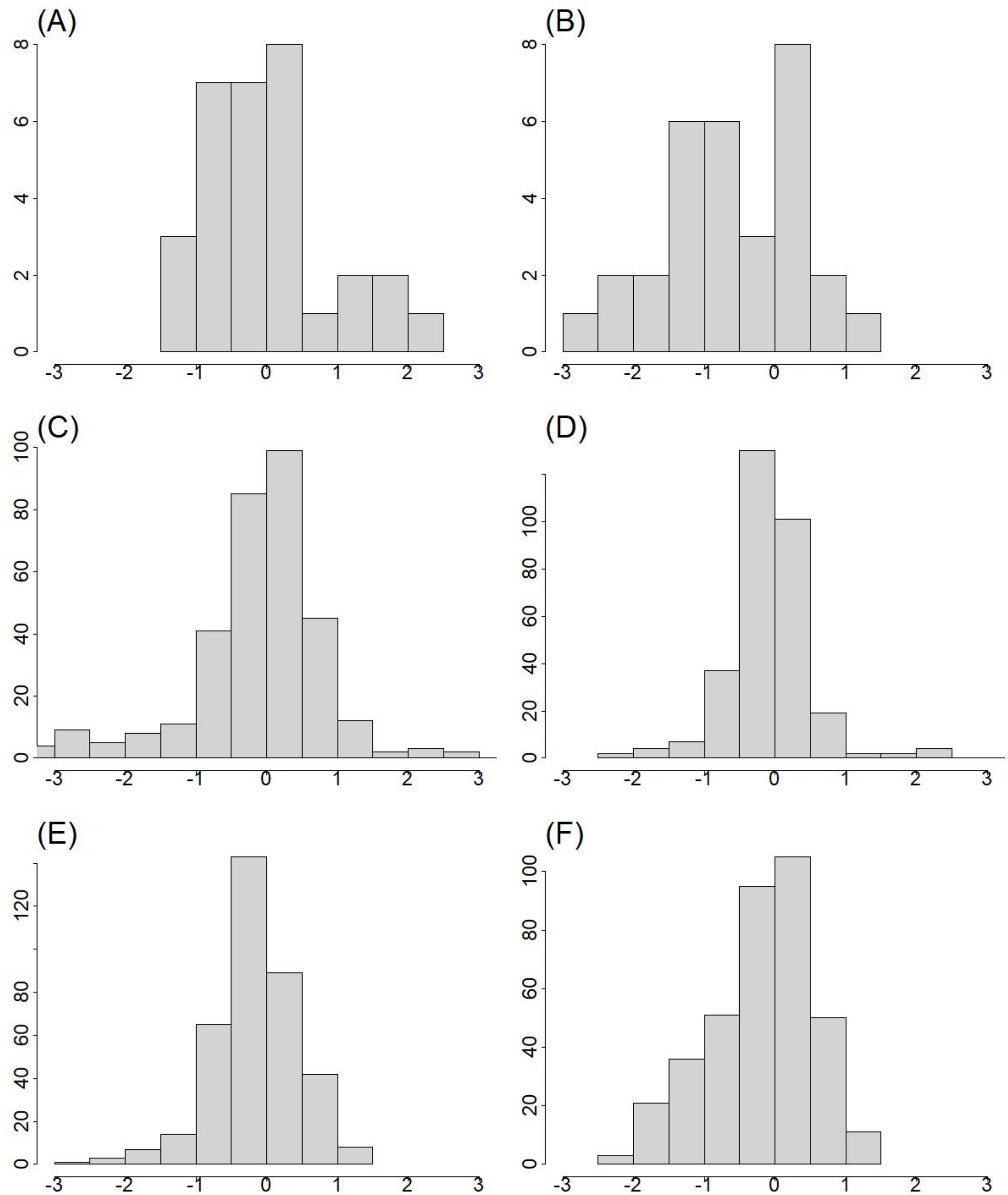
(A)
(B)
(C)
(D)
(E)
(F)

Fig. C2. Histogram plots of one step ahead (OSA) residuals of (A) total trap net catch on the log-scale, (B) total gill net catch on the log-scale, (C) trap net proportions at age and(D) gill net proportions at age, and the process variability at age of the (E) trap net catchability and (F) gill net catchability.

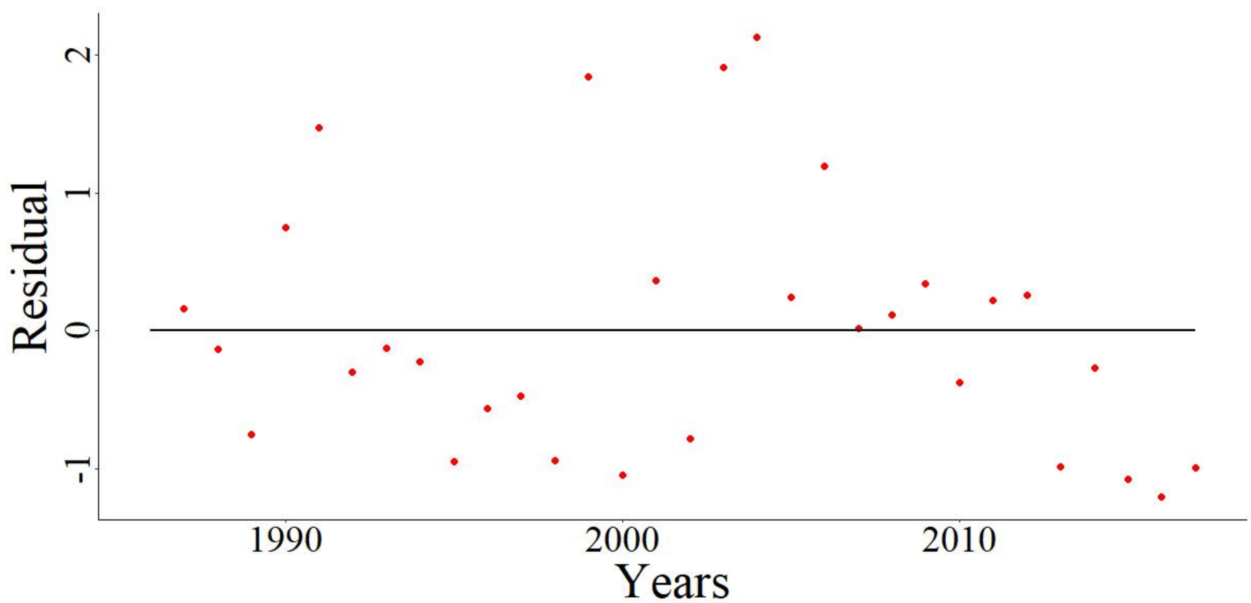

Fig. C3. One step ahead (OSA) residuals of total log-scale catch of the trap net fishery by year. Observed catch was modeled as a lognormal distribution with mean equal to the expected catch and standard deviation 0.067.

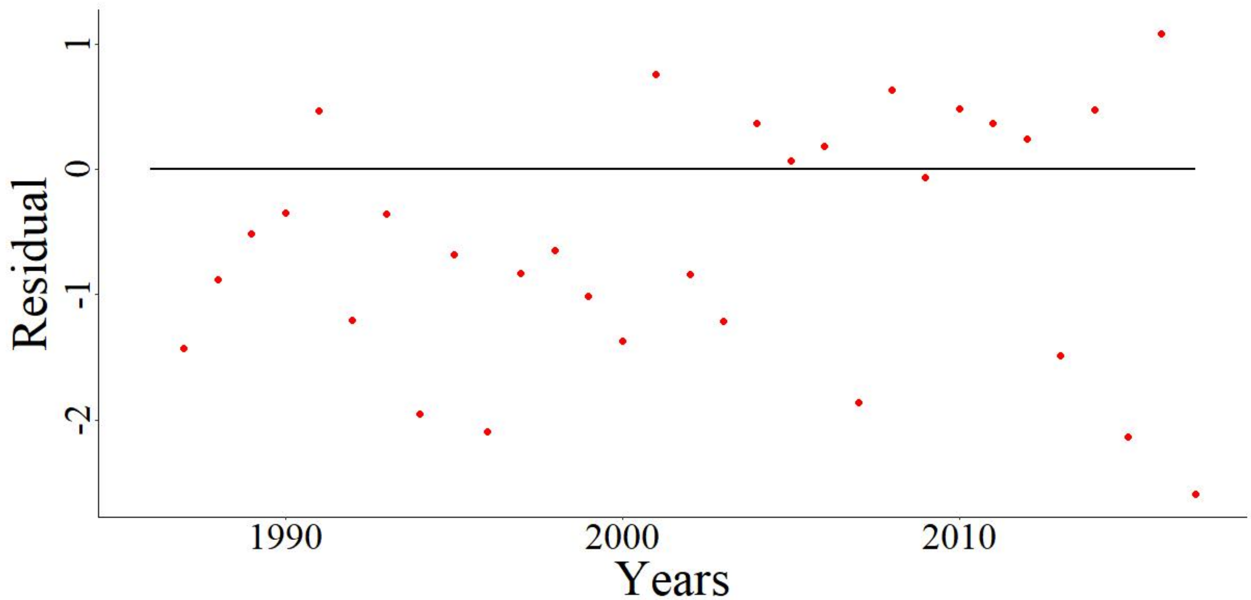

Fig. C4. One step ahead (OSA) residuals of total log-scale catch of the gill net fishery by year. Observed catch was modeled as a lognormal distribution with mean equal to the expected catch and standard deviation 0.067.

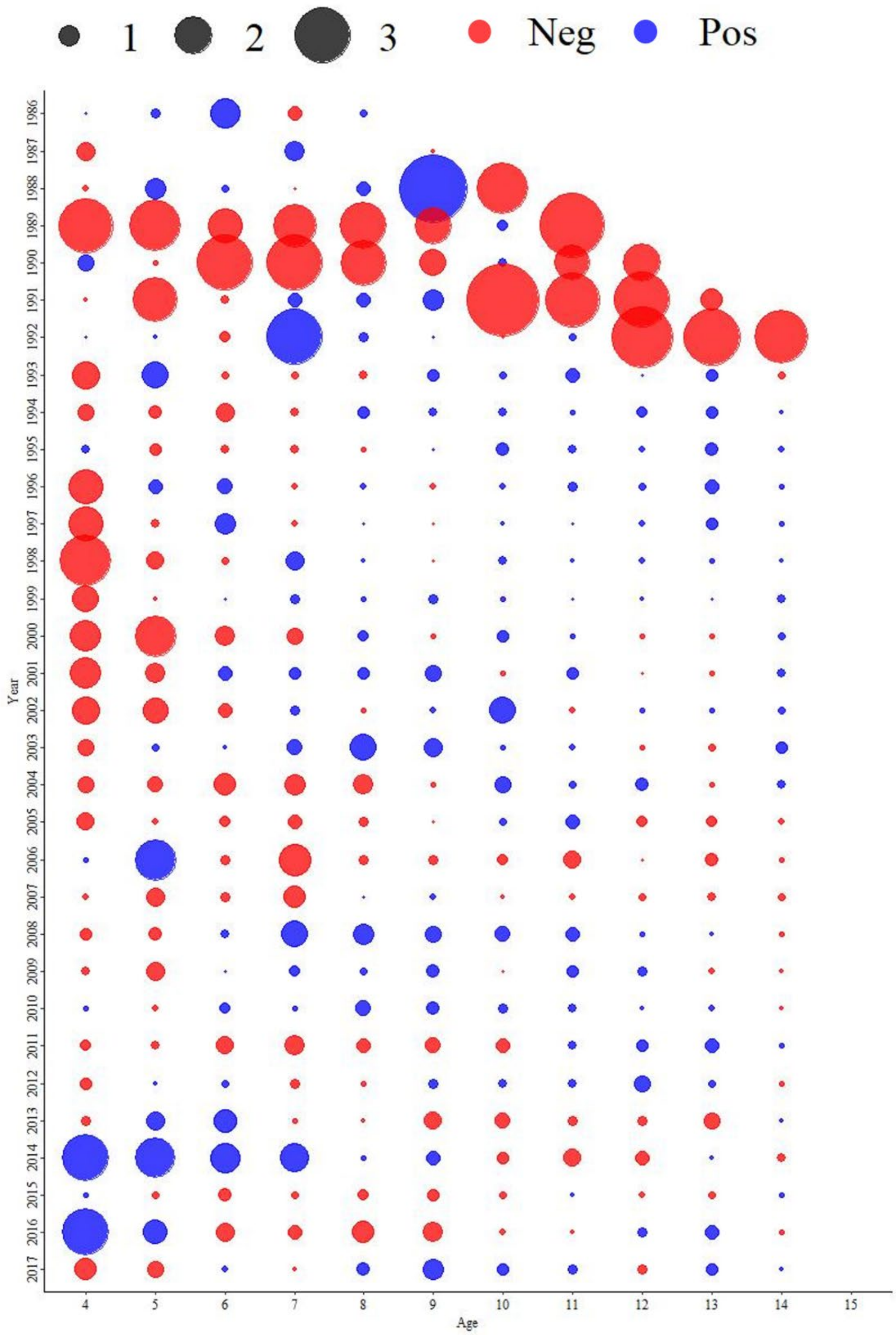

Fig. C5. One step ahead (OSA) residuals of proportions at age of the trap net fishery. Observed proportions were modeled as a multinomial distribution with year-specific effective sample size. No residuals were reported for year and age combination where the expected and observed value was 0 (older ages in the first 6 years) or for age 15+, because the way OSA residuals are calculated does not allow for estimates in the oldest age.

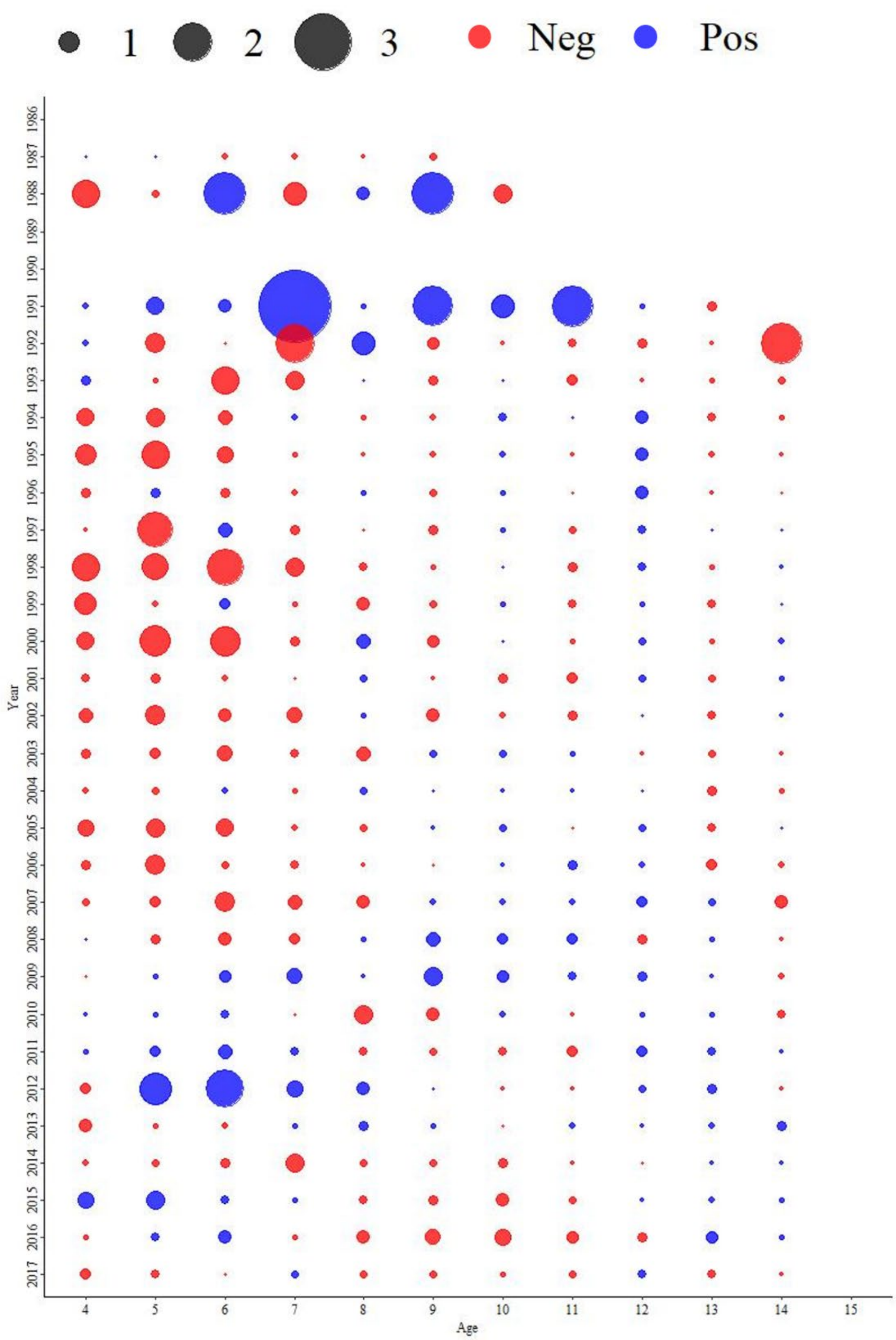

Fig. C6. One step ahead (OSA) residuals of proportions at age of the gill net fishery. Observed proportions were modeled as a multinomial distribution with year-specific effective sample size. No residuals were reported for year and age combination where the expected and observed value was 0 (older ages in the first 6 years) or for age 15+, because the way OSA residuals are calculated does not allow for estimates in the oldest age. Note that years 1986, 1989, and 1990 are also absent because the sample size was zero.

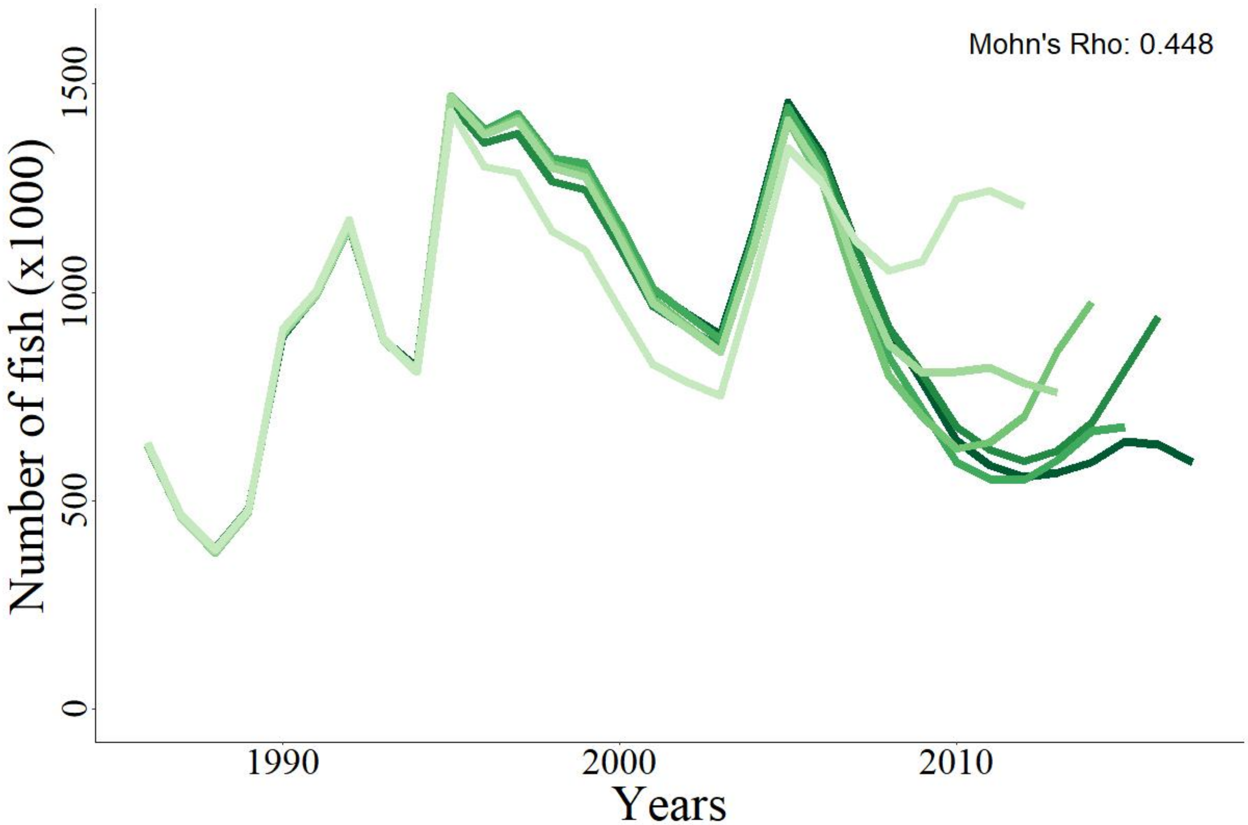

Fig. C7. Retrospective analysis of estimated recruitment in number of fish. The SSM model was refit after removing sequential years of the most recent observations. Dark colors indicate more complete data sets and lighter colors indicate less complete data sets.

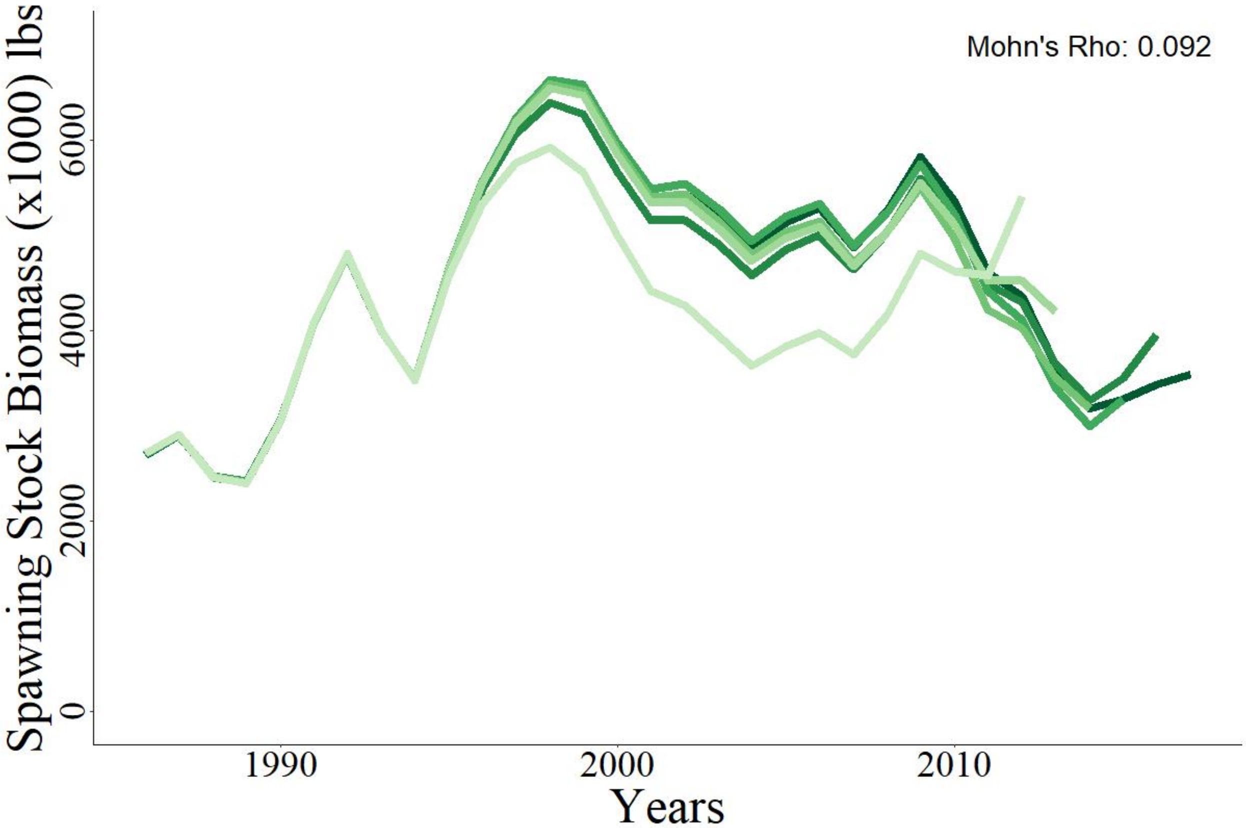

Fig. C8. Retrospective analysis of estimated spawning stock biomass. The SSM model was refit after removing sequential years of the most recent observations. Dark colors indicate more complete data sets and lighter colors indicate less complete data sets.

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Tables and Figures

Table 1. Symbols used in the text, appendices, tables, and figures. Whether the symbol is used in the statistical catch at age model (SCA), the state-space model (SSM), or both, is indicated. The value is provided for indices and time and age invariant data.

Symbol	Description	Usage	Value(s)
Index Variables			
y	Year	Both	1986-2017
a, $\tilde{a}$	Age	Both	4-15+
G	Fishery	Both	g- gill net, t-trap net
Data and Priors			
$E_{y,G}$	Observed effort by year and fishery	Both	See Fig. 2
$\tilde{C}_{y,G}$	Observed harvest by year and fishery	Both	
$\tilde{P}_{a,y,G}$	Observed proportions by age, year, and fishery	Both	
$\widetilde{M}$	Observed natural mortality	SSM	0.2
$\widehat{M}$	Median of prior on natural mortality	SCA	0.2
σ_M	Standard deviation of observed or prior natural mortality	Both	0.1
$m_{a,y}$	Maturity by age and year	Both	
$W_{a,y}^{(spawn)}$	Weight at the time of spawning by age and year	Both	
e	Average number of eggs per kilogram	SCA	19937
f	Average proportion of females in spawning population	SCA	0.4845
φ_G	Standard deviation multiplier for fishery-specific catchability, $q_{y,G}$, process variability	SCA	4
φ_s	Standard deviation multiplier for trap net selectivity parameter $p_{1,y,t}$ process variability	SCA	1.0
φ_R	Standard deviation multiplier for recruitment process variability	SCA	15
φ_{CG}	Standard deviation multiplier for total catch observation error	SCA	1.5
σ_{CG}	Standard deviation of likelihood of total catch	SSM	0.067
n_G	Effective sample size of multinomial likelihood of observing given proportion at age of catch	Both	See Appendix B, Table B1
Parameters and State Variables			
M	Instantaneous natural mortality	Both	
σ_G	Standard deviation of process variability of fishery-specific catchability	SSM	
ρ_G	Correlation coefficient (between ages) of process variability of fishery-specific catchability	SSM	
σ_R	Standard deviation of process variability of recruitment	SSM	
$\varepsilon_y^{(R)}$	Process variability of recruitment	SSM	
$\boldsymbol{\varepsilon}_y^{(G)}$	Vector of process variability of fishery-specific catchability	SSM	
$q_{y,G}$	Catchability by year and fishery	SCA	

σ	Baseline standard deviation for process variability and observation error	SCA	
$p_{1,1986,t}$	Trap net selectivity inflection point parameter in the first year	SCA	
$\varepsilon_y^{(s)}$	Process variability of trap net selectivity parameter	SCA	
$p_{1,g}$	Gill net selectivity parameter	SCA	
$p_{2,G}$	Trap and gill net selectivity parameters	SCA	
$\bar{R}$	Average recruitment and abundance in 1986	SCA	
D_y	Deviations by year from average recruitment	SCA	
d_a	Deviations by age from average abundance in 1986	SCA	
α	Ricker stock recruitment parameter (density-independent parameter)	SCA	
β	Ricker stock recruitment parameter (density-dependent parameter)	SCA	
Derived Quantities			
$N_{a,y}$	Abundance by age and year	Both	
$\widehat{N}_{4,y}$	Predicted abundance of age 4 individuals by year (recruitment)	SCA	
$F_{a,y,G}$	Instantaneous fishing mortality by age, year, and fishery	Both	
$\boldsymbol{q}_{y,G}$	Vector of age-specific catchability by year and fishery	SSM	
$s_{a,y,G}$	Selectivity by age, year, and fishery	SCA	
$p_{1,y,t}$	Trap net selectivity inflection point parameter after the first year (y>1986)	SCA	
$Z_{a,y}$	Instantaneous total mortality by age and year	Both	
$\bar{Z}_a$	Average instantaneous total mortality by age from 1986-1988	SCA	
$C_{a,y,G}$	Expected harvest by age, year, and fishery	Both	
$P_{a,y,G}$	Expected proportions by age, year, and fishery	Both	
$B_y^{(Spawn)}$	Spawning stock biomass by year	Both	
ϵ_y	Spawning stock size in eggs by year	SCA	
T	Total objective function value	Both	
σ_a	Standard deviation of multivariate normal random walk deviations of fishery-specific catchability	SSM	Equals σ_G for each fishery
$\boldsymbol{\Sigma}_G$	Covariance matrix of process variability of fishery-specific catchability	SSM	
σ_s	Standard deviation of process variability of trap net selectivity parameter	SCA	

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Table 2. Equations used in the statistical catch at age model (SCA), the state-space model (SSM), or both. Note that though equations 2.5a and 2.5b appear identical, each contributes to a different part of the objective function total, which is an important distinction in the integrated likelihood framework.

Index	Description	Equation	Usage
Process Model			
1.1	Recruitment random walk	$\log N_{4,y} = \log N_{4,y-1} + \varepsilon_y^{(R)};\ \varepsilon_y^{(R)} \sim N(0, \sigma_R^2)$	SSM
1.2	Abundance at age 4-9 in initial year	$\log N_{a,1986} = \log N_{4,1986-(a-4)} - \sum_{4}^{a-1} \log \bar{Z}_a, 4 < a \leq 9$	SSM
1.3	Abundance at age 9+ in initial year	$\log N_{a,1986} = 0, a > 9$	Both
1.4	Abundance at age exponential decay with plus group	$\log N_{a,y} = \log N_{a-1,y-1} - Z_{a-1,y-1}, 4 \leq a < A$ $\log N_{A,y} = \log(N_{A-1,y-1}\, e^{-Z_{A-1,y-1}} + N_{A,y-1} e^{-Z_{A,y-1}})$	Both
1.5	Total instantaneous mortality	$Z_{a,y} = M + \sum_{G=g,t} F_{a,y,G}$	Both
1.6a	Fishing mortality	$F_{a,y,G} = q_{y,G} E_{y,G} s_{a,y,G}, G = g, t$	SCA
1.6b	Fishing Mortality	$F_{a,y,G} = q_{a,y,G} E_{y,G}, G = g, t$	SSM
1.7a	Year-specific catchability random walk	$\log q_{y+1,G} = \log q_{y,G} + \varepsilon_y^{(G)};\ \varepsilon_y^{(G)} \sim N(0, \sigma_G^2), G = g, t$	SCA
1.7bi	Year- and age- specific vector of catchability random walk	$\log \boldsymbol{q}_{y,G} = \log \boldsymbol{q}_{y-1,G} + \boldsymbol{\varepsilon}_y^{(G)};\ \boldsymbol{\varepsilon}_y^{(G)} \sim N(0, \boldsymbol{\Sigma}_G), G = g, t$	SSM
1.7bii	Correlated error of catchability random walk	$\boldsymbol{\Sigma}_{a,\tilde{a}} = \rho^{\lvert a-\tilde{a}\rvert} \sigma_a \sigma_{\tilde{a}}, 4 < a < A, 4 < \tilde{a} < A$	SSM
1.8	Spawning stock biomass	$B_y^{(Spawn)} = \sum_{i=4}^{A} m_{i,y} W_{i,y}^{(spawn)} \log N_{i,y}$	Both
Observation Model			
2.1	Baranov catch equation	$C_{a,y,G} = \frac{F_{a,y,G}}{Z_{a,y}} N_{a,y}\left(1 - \exp(-Z_{a,y})\right), G = g, t$	Both
2.2	Yearly catch proportions at age	$P_{a,y,G} = \frac{C_{a,y,G}}{\sum_{a=1}^{A} C_{a,y,G}}, G = g, t$	Both
Negative Log Likelihoods			
3.1	Total objective function on the log-scale is the sum of prior/penalty and data likelihood components	$T = \sum NLP + \sum NLL$	Both
3.2a	Recruitment deviations from those expected by Ricker curve (see Appendix B)	$\mathrm{NLP}^{(R)} = \sum_{i=1991}^{2017} \frac{1}{2\sigma_R^2}\left(\log \frac{\hat{N}_{4,i}}{N_{4,i}}\right)^2 + \log \sigma_R$	SCA

3.2b	Recruitment deviations from those expected around 0	$\mathrm{NLP}^{(R)} = \sum_{i=1981}^{2017} \frac{1}{2\sigma_R^2}\left(\varepsilon_i^{(R)}\right)^2 + \log\sigma_R$	SSM
3.3a	Fishery-specific deviations in catchability following a random walk	$\mathrm{NLP}^{(G)} = \sum_{i=1986}^{2017} \frac{1}{2\sigma_G^2}\left(\varepsilon_i^{(G)}\right)^2 + \log\sigma_G\,, G = g, t$	SCA
3.3b	Fishery-specific deviations in vector of catchability at age following a random walk	$\mathrm{NLP}^{(G)} = \sum_{i=1986}^{2017} {}^{1}\!/_{2}\, \boldsymbol{\varepsilon}_y^{(G)\prime} \Sigma_T{}^{-1} \boldsymbol{\varepsilon}_y^{(G)} + \log\sqrt{\lvert\boldsymbol{\Sigma}_G\rvert}\,, G = g, t$	SSM
3.4	Deviations for random walk for trap net selectivity parameter	$\mathrm{NLP}^{(s)} = \sum_{i=1986}^{2017} \frac{1}{2\sigma_s^2}\left(\varepsilon_i^{(s)}\right)^2 + \log\sigma_s$	SCA
3.5a	Penalty on natural mortality from deviating from median of the prior	$\mathrm{NLP}^{(M)} = \frac{1}{2\sigma_M^2}\left(\log\widehat{M} - \log M\right)^2 + \log\sigma_M$	SCA
3.5b	Likelihood of observing a given natural mortality value based on assumed true value	$\mathrm{NLL}^{(M)} = \frac{1}{2\sigma_M^2}\left(\log\widetilde{M} - \log M\right)^2 + \log\sigma_M$	SSM
3.6	Likelihood of observing the given total catch based on an assumed true value	$\mathrm{NLL}^{(CG)} = \sum_{i=1986}^{2017} \frac{1}{2\sigma_{CG}^2}\left(\log\frac{C_{i,G}}{\tilde{C}_{i,G}}\right)^2 + \log\sigma_{CG}\,, G = g, t$	Both
3.7	Likelihood of observing the given proportions at age of catch based on assumed true values	$\mathrm{NLL}^{(PG)} = -\sum_{i=1986}^{2017}\sum_{j=4}^{A} n_{i,G}\tilde{P}_{j,i,G}\, \log P_{j,i,G}\,, G = g, t$	Both

Table 3. Point estimates and asymptotic standard errors of fixed effect parameters in the State-space model (SSM) for Lake Michigan lake whitefish in WFM-03.

Parameter (Symbol)	Estimate	Standard Error
M	0.1896	0.0184
σ_R	0.2474	0.0428
σ_t	0.3652	0.0442
σ_g	0.3905	0.0492
ρ_t	0.8438	0.0502
ρ_g	0.9142	0.0356

Table 4. Estimates of derived quantities in the state-space model (SSM) and statistical catch at age (SCA) model for Lake Michigan lake whitefish in WFM-03.

Quantity	SCA Estimate	SSM Estimate	Percent (%) difference
Average Abundance	2,633,377	3,001,214	13.97
Maximum Abundance	4,431,335	4,885,740	10.25
Minimum Abundance	953,555	1,126,510	18.14
Abundance Range	3,477,780	3,759,230	8.10
Average Recruitment	807,254	910,279	12.76
Average Recruitment in Terminal 10 years	492,468	650,837	32.16
Minimum Recruitment	252,249	385,213	52.71
Maximum Abundance	1,545,150	1,460,345	-5.49
Recruitment Range	1,292,901	1,075,132	-16.84
Average Spawning Stock Biomass (SSB) (lbs)	3,931,830	4,489,802	14.19
Minimum SSB (lbs)	2,182,870	2,418,414	10.79
Maximum SSB (lbs)	5,985,860	6,542,546	9.30
SSB Range (lbs)	3,802,990	4,124,132	8.44
Average Total Mortality	0.647	0.543	-16.07
Maximum Total Mortality	0.303	0.268	-11.55
Minimum Total Mortality	1.288	1.211	-5.98
Total Mortality Range	0.985	0.942	-4.37
Average Trap Net Mortality	0.251	0.159	-36.65
Maximum Trap Net Mortality	0.060	0.036	-40.00
Minimum Trap Net Mortality	0.485	0.306	-36.91
Trap Net Mortality Range	0.424	0.270	-36.32
Average Gill Net Mortality	0.202	0.195	-3.47
Maximum Gill Net Mortality	0.013	0.005	-61.54
Minimum Gill Net Mortality	0.704	0.745	5.82
Gill Net Mortality Range	0.691	0.740	7.09
Spawning Potential Ratio (SPR)	0.53	0.63	18.87

Table 5. Results of sensitivity analysis. The maximum likelihood estimates of fixed effect parameters are reported for each scenario as well as the percent (%) difference relative to the baseline.

Scenario	M	% Diff	σ_R	% Diff	σ_t	% Diff	σ_g	% Diff	ρ_t	% Diff	ρ_g	% Diff
$\sigma_{CG} = 0.067$ (Baseline)	0.1896		0.2474		0.3652		0.3905		0.8438		0.9142	
$\sigma_{CG} = 0.034$	0.1899	0.18	0.2476	0.09	0.3696	1.2	0.4032	3.26	0.8465	0.32	0.9195	0.58
$\sigma_{CG} = 0.100$	0.1896	-0.17	0.2471	-0.2	0.3603	-2.51	0.3711	-7.96	0.8406	-0.7	0.9052	-1.55

Fig. 1. Lake whitefish management units of the 1836 Treaty-Ceded Waters of Lakes Superior, Huron, and Michigan, including the management region of interest, WFM-03, in northern Lake Michigan. Reproduced from Caroffino and Barton (2019).

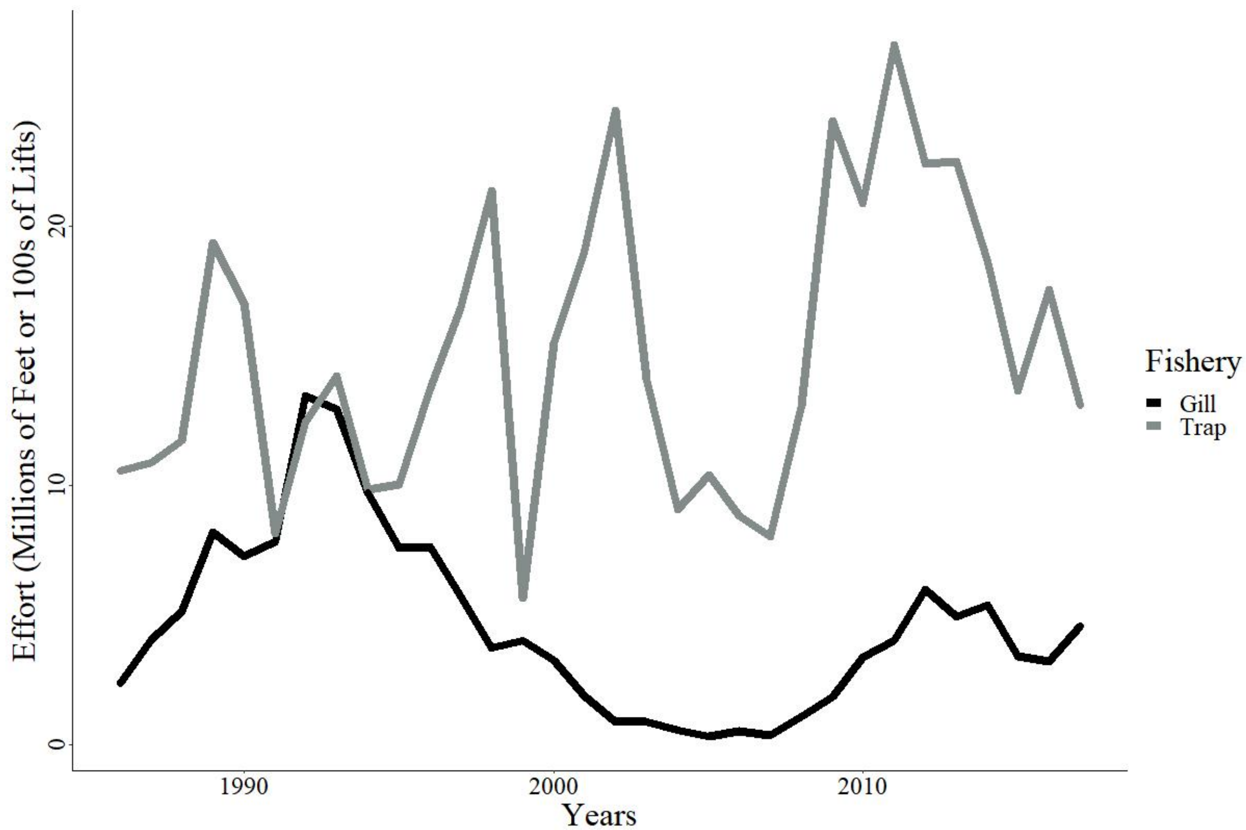

Fig. 2: Fishery effort of the gill net and trap net fisheries on Lake Michigan lake whitefish in region WFM-03 from 1986-2017.

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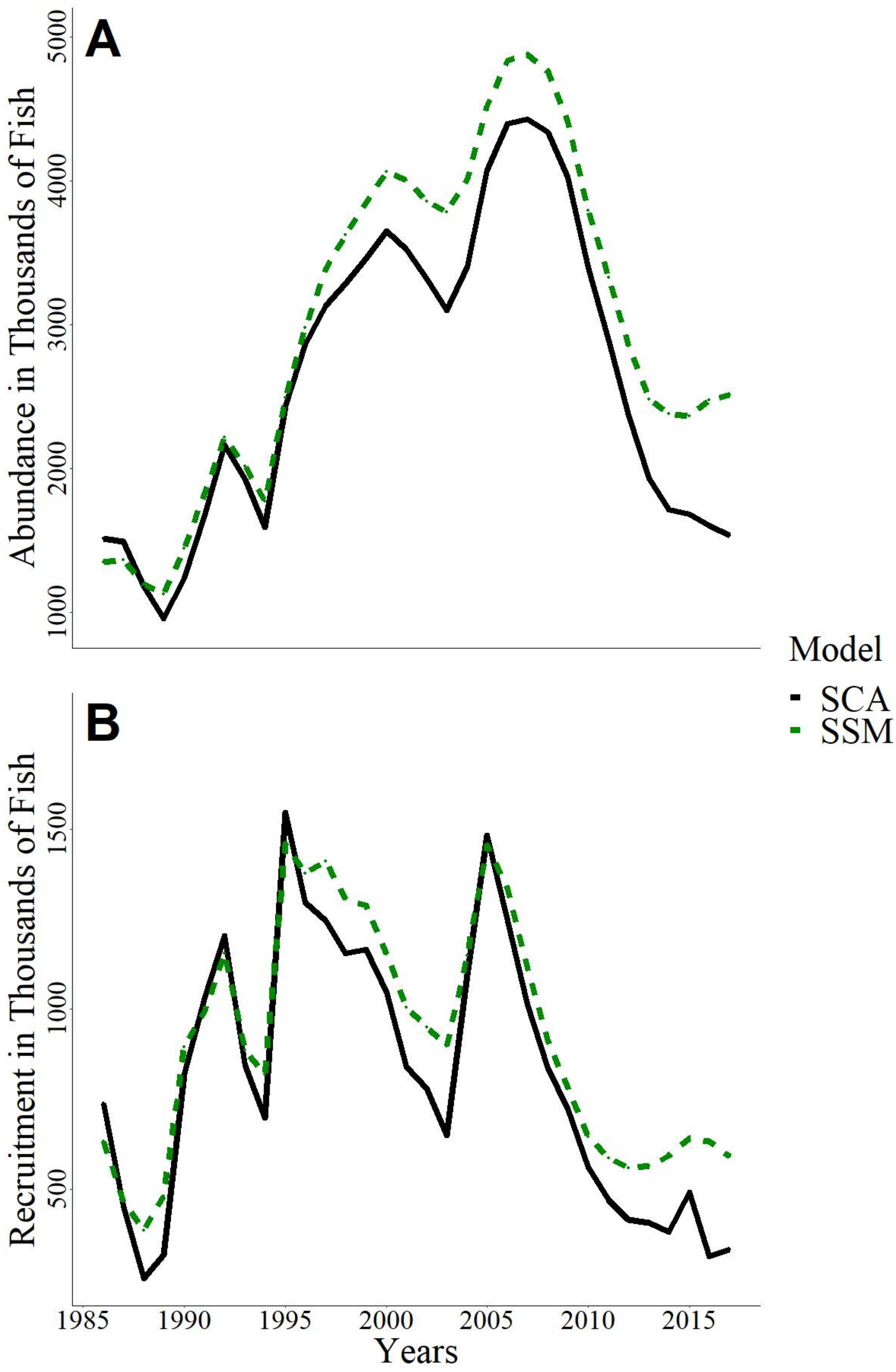

A
B
Abundance in Thousands of Fish
Recruitment in Thousands of Fish
5000
4000
3000
2000
1000
1500
1000
500
1985
1990
1995
2000
2005
2010
2015
Years
Model
SCA
SSM

Fig. 3. Estimates of (A) abundance and (B) recruitment of age 4 individuals of Lake Michigan lake whitefish in WFM-03 from 1986-2017, from the statistical catch at age (SCA) model (black, solid), and the state-space model (SSM) (green, dashed).

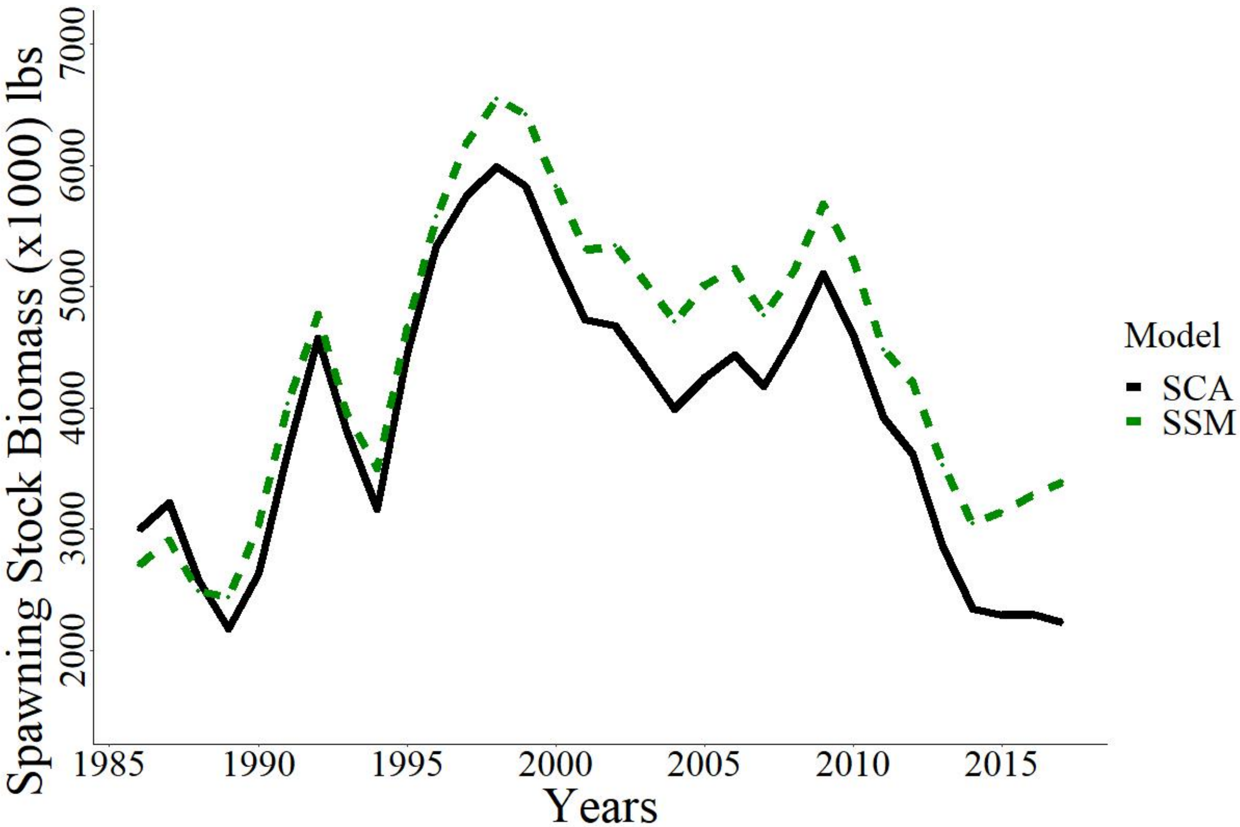

Fig. 4. Estimates of spawning stock biomass of Lake Michigan lake whitefish in WFM-03 from 1986-2017, from the statistical catch at age (SCA) model (black, solid), and the state-space model (SSM) (green, dashed).

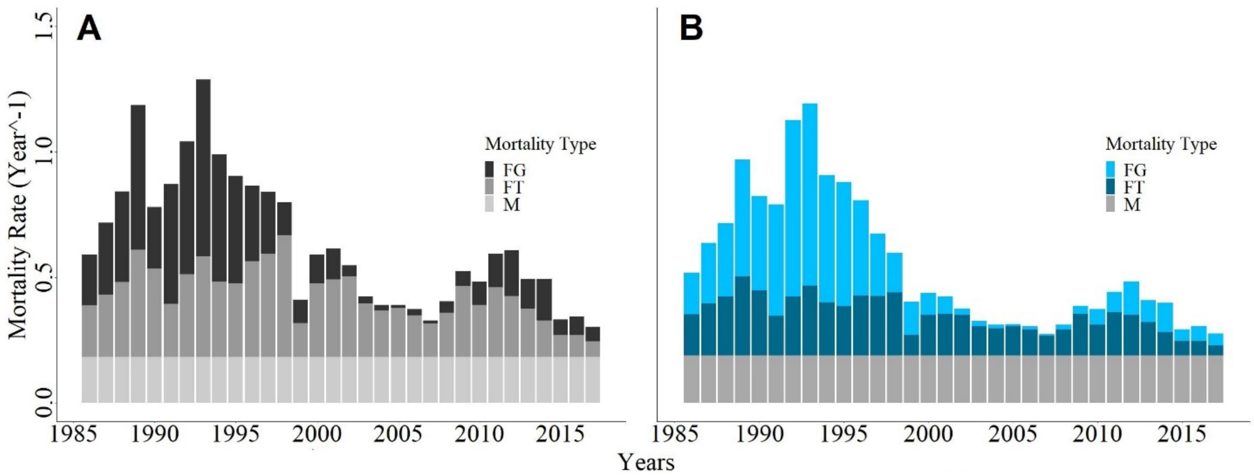

Fig. 5. Estimated instantaneous fishing mortality rate of the gill net fishery (FG), the trap net fishery (FT) and the natural mortality rate (M) over time for (A) the statistical catch at age model (SCA) and (B) the state-space model (SSM). The instantaneous fishing mortality rate was averaged across ages 4-15+ for each year, and instantaneous natural morality rate was age- and year- invariant.

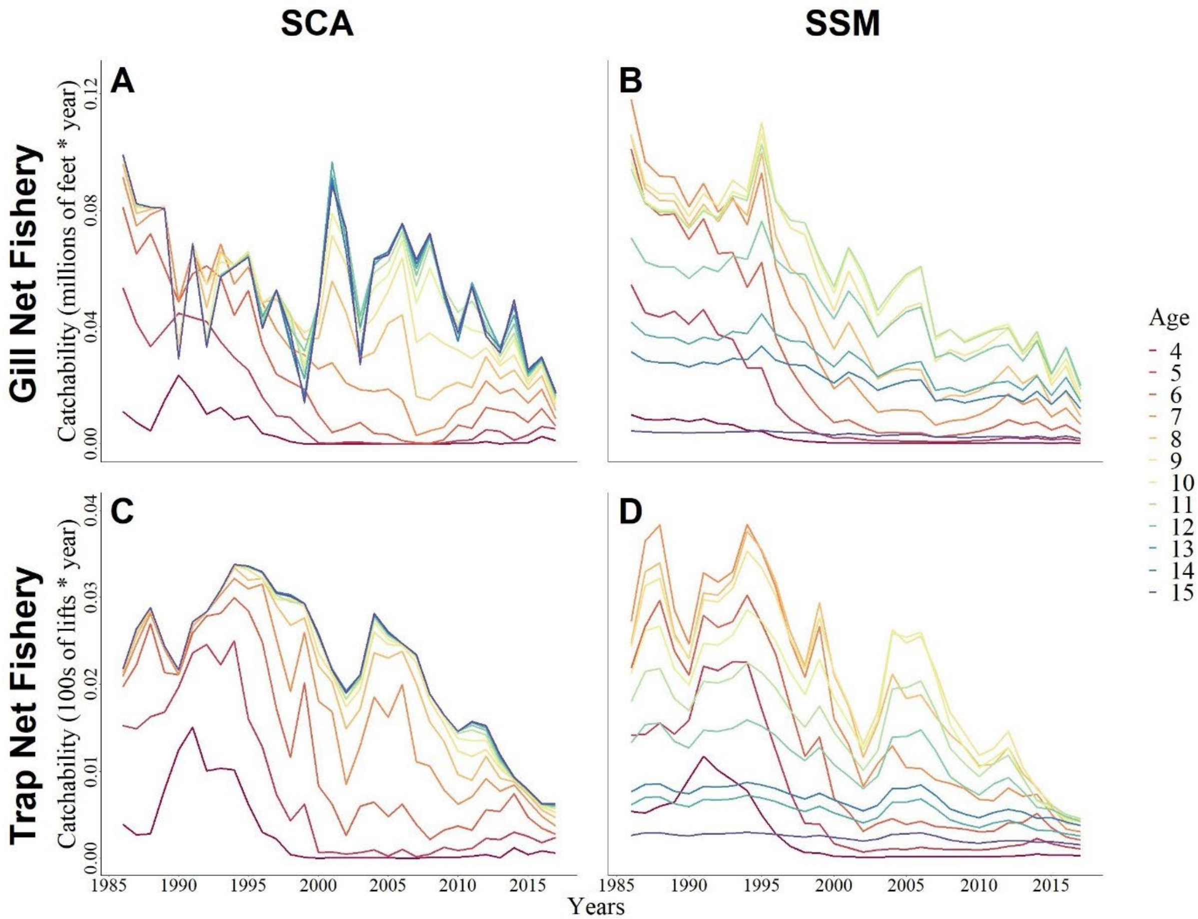

Fig. 6. Estimated catchability over years for each age (on scale from red to purple from age 4 to 15+) of the (A) gill net and (C) trap net fishery in the statistical catch at age (SCA) model, and the (B) gill net and (D) trap net fishery in the state-space model (SSM).

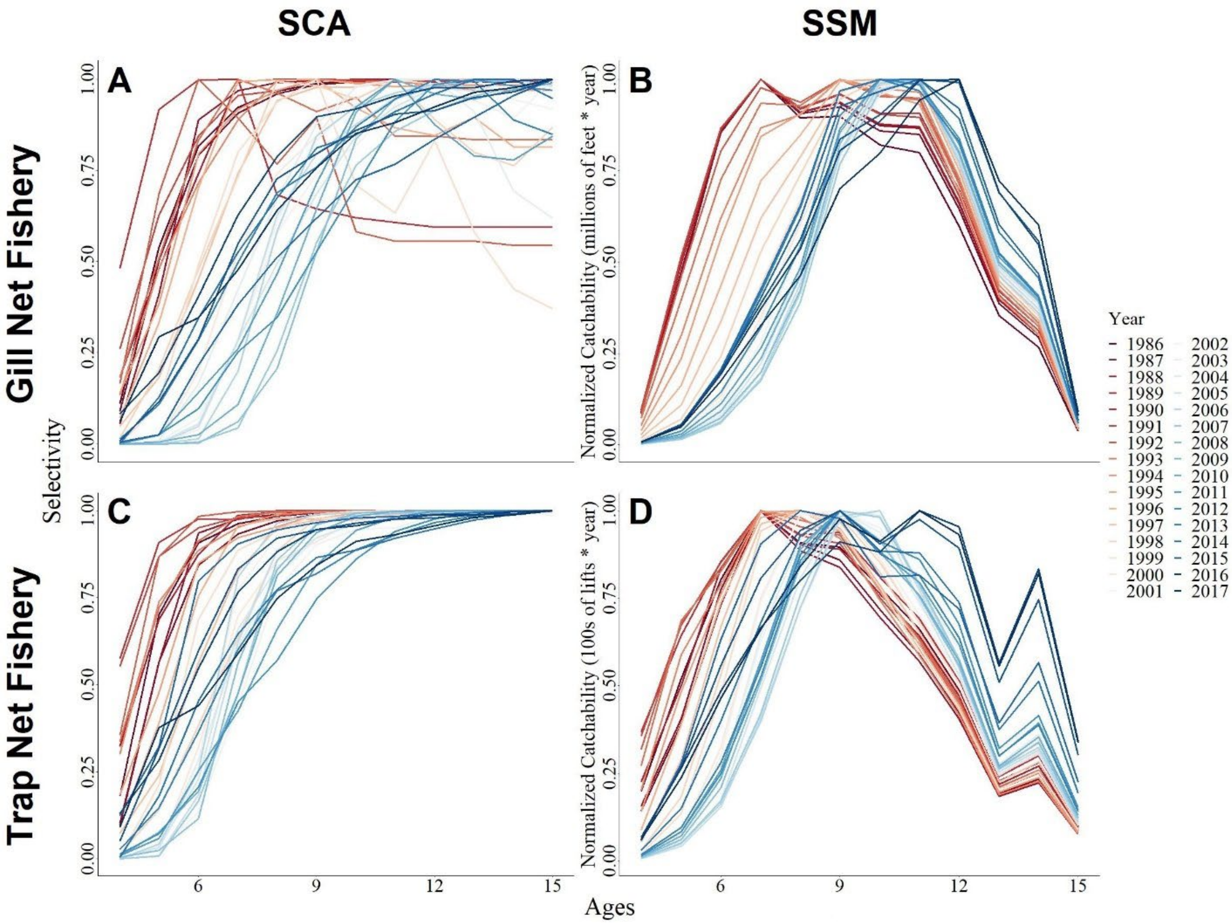

Fig. 7. Estimated selectivity over ages for each year (on scale from red for early years to blue for later years) of the (A) gill net and (C) trap net fishery in the statistical catch at age (SCA) model, and of the (B) gill net and (D) trap net fishery in the state-space model (SSM). Selectivity was obtained by normalizing age-specific catchability such that the maximum value for each year was 1.